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Analysis of trade-offs between threats of invasion by nonnative brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*)

Douglas P. Peterson, Bruce E. Rieman, Jason B. Dunham, Kurt D. Fausch, and Michael K. Young

Abstract: Native salmonid fishes often face simultaneous threats from habitat fragmentation and invasion by nonnative trout species. Unfortunately, management actions to address one may create or exacerbate the other. A consistent decision process would include a systematic analysis of when and where intentional use or removal of barriers is the most appropriate action. We developed a Bayesian belief network as a tool for such analyses. We focused on native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and nonnative brook trout (*Salvelinus fontinalis*) and considered the environmental factors influencing both species, their potential interactions, and the effects of isolation on the persistence of local cutthroat trout populations. The trade-offs between isolation and invasion were strongly influenced by size and habitat quality of the stream network to be isolated and existing demographic linkages within and among populations. An application of the model in several sites in western Montana (USA) showed the process could help clarify management objectives and options and prioritize conservation actions among streams. The approach can also facilitate communication among parties concerned with native salmonids, nonnative fish invasions, barriers and intentional isolation, and management of the associated habitats and populations.

Résumé : Les poissons salmonidés indigènes font souvent face simultanément à une double menace représentée par la fragmentation des habitats et l'invasion de salmonidés non indigènes. Malheureusement, les aménagements faits pour régler un de ces problèmes peuvent faire surgir ou exacerber le second. Un processus de décision cohérent devrait inclure une analyse systématique du moment et de l'endroit les plus appropriés pour l'érection ou le retrait de barrières. Nous avons mis au point un réseau de croyance bayésien pour servir d'outil pour ces analyses. Nous nous sommes intéressés spécifiquement à la truite fardée (*Oncorhynchus clarkii lewisi*) indigène du versant occidental et à l'omble de fontaine (*Salvelinus fontinalis*) non indigène; nous avons tenu compte des facteurs du milieu qui influencent les deux espèces, de leurs interactions potentielles et des effets de l'isolement sur la persistance des populations locales de truites fardées. Les compromis entre l'isolement et l'invasion sont fortement influencés par la taille et la qualité des habitats du réseau de cours d'eau à isoler, ainsi que par les liens démographiques établis à l'intérieur des populations et entre elles. L'utilisation du modèle dans plusieurs sites de l'ouest du Montana (É.-U.) montre que le processus peut servir à éclaircir les objectifs et les options de l'aménagement et à établir les priorités des initiatives de conservation dans les différents cours d'eau. Cette méthode peut aussi faciliter la communication entre les divers intervenants préoccupés par les salmonidés indigènes, les invasions de poissons non indigènes, les barrières et l'isolement délibéré, ainsi que par l'aménagement des habitats et des populations associés.

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Introduction

Indigenous stream fishes, particularly salmonids, are in decline in many portions of western USA. Habitat fragmentation and invasion of nonnative fishes are primary contributors to these declines (Young 1995; Rieman et al. 2003; Fausch et al. 2006), but attempts to ameliorate their different effects may elicit different and often conflicting management approaches.

Widespread fragmentation of habitats and isolation of populations has been caused by habitat degradation (e.g., decreased water quality and quantity) and fish passage barriers associated with irrigation diversions, dams, and road crossings with impassable culverts that number in the thousands across the region (US General Accounting Office (US GAO) 2001; Clarkin et al. 2003). As a result, many populations of native salmonids are now restricted to headwater streams (Fausch et al. 2006; Neville et al. 2006). Population isolation can lead to loss of genetic diversity, limited expression of life history diversity, reduced population resilience, and ultimately to local extinction (see Fausch et al. 2006 for a review). Reversing habitat degradation can be slow, technically and politically difficult, and expensive (Williams et al. 1997). On the other hand, where habitats remain in relatively good condition, reversing habitat fragmentation and population isolation may only require removal or modification of a fish passage barrier. The ultimate cost and benefit, however, must be considered in the context of other threats, particularly encroachment by nonnative fishes.

Nonnative fishes have been widely introduced in western US streams since the late 1800s. Many nonnative species now occur in main-stem rivers (Lee et al. 1997), but of particular concern for native salmonids is the widespread invasion of brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Oncorhynchus mykiss*) into mid- and higher-elevation streams (e.g., Thurow et al. 1997; Schade and Bonar 2005). Nonnative trout can displace native species via hybridization (e.g., Allendorf et al. 2001), competition, or predation (e.g., Dunham et al. 2002*a*; Peterson and Fausch 2003). These nonnative species pose an acute threat to the native salmonids that are increasingly restricted to headwater streams (Dunham et al. 2002*a*; Fausch et al. 2006). Because nonnatives may continue to spread, many remnant populations of native salmonids remain at risk. As a result, many biologists install fish migration barriers, a strategy called isolation management (e.g., Kruse et al. 2001; Novinger and Rahel 2003).

The conundrum is that removal of migration barriers to connect native populations to larger stream networks could allow upstream invasions of nonnative fishes, while installing migration barriers to preclude these invasions may exacerbate effects of habitat fragmentation and population isolation. Both actions could threaten native species and integrity of aquatic systems, but fish biologists may employ both barrier installation and barrier removal strategies across the western USA without evaluation of the opposing threats. The potential conflicts highlight a challenge in native fish conservation.

Because resources for conservation management are limited, effective prioritization is important. Trade-offs may be relatively clear to biologists and managers with intimate knowledge of a particular system, and their efforts can be focused effectively. Elsewhere, the trade-offs may be more ambiguous or the data and experience more limited, and the result may be a decision that is influenced more by personal philosophy or public pressure than by knowledge. When the differences in these decisions cannot be clearly supported and articulated, the process can appear inconsistent and arbitrary to the public or the administrators controlling funding (US GAO 2001). A formal decision process could help.

Methods for assessment of barriers to fish passage are widely available (Clarkin et al. 2003), but tools to evaluate relative risks and trade-offs or to prioritize work are not. The limitation is not necessarily in knowledge of the relevant biology. Research on fish populations upstream of fish passage barriers, for example, showed the probability of extinction increases as a function of decreasing habitat area and time (e.g., Morita and Yamamoto 2002). Similar work exists on the distribution and interaction of nonnative and native salmonid species (e.g., Paul and Post 2001; Peterson et al. 2004). Existing knowledge, then, provides a foundation to consider the risks inherent in intentional isolation or continuing species invasions.

Fausch et al. (2006) synthesized much of the current knowledge, proposed a framework to consider trade-offs in the installation or removal of barriers, and provided general guidelines for individual decisions and prioritization of action among streams. A central conclusion was that trade-offs between the relative threats of invasion or isolation depend very much on environmental context. Application of these guidelines in complex environments, however, requires consideration of multiple interacting factors that may be difficult to address consistently, particularly when there is uncertainty about the conditions influencing the trade-offs. A Bayesian belief network (BBN) is one method that could be used to formalize the evaluation.

BBNs (Pearl 1991; Jensen 1996) increasingly are being used to provide formal decision support for natural resource issues (Reckhow 1999; Marcot et al. 2001; Marcot 2006), including fisheries management (e.g., Lee and Rieman 1997; Rieman et al. 2001; Borsuk et al. 2006). BBNs can be used to evaluate relative differences in predicted outcomes among management decisions. They are appealing because their basic structure (a box-and-arrow diagram that depicts hypothesized causes, effects, and ecological interactions) can be readily modified to reflect new information or differences in perceptions about key relationships. Moreover, BBNs can incorporate information from a variety of sources, such as empirical data, professional opinion, and output from process-based models. Outcomes also are expressed as probabilities, so uncertainty is explicit. In addition, BBNs are conceptually straightforward to build and use, so biologists can explore a variety of management scenarios in different ecological contexts and then quantify and communicate these options to decision makers (Marcot et al. 2006; Marcot 2007).

Our goal was to formalize an evaluation of trade-offs between intentional isolation and invasion, relevant to conservation of native salmonids. We focused on persistence of native westslope cutthroat trout (hereafter WCT, *Oncorhynchus clarkii lewisi*), potential invasion and subsequent effects of nonnative brook trout, and the primary environmental and anthropogenic factors influencing both species and their interactions. Our objectives were to develop and explore the application of a BBN as a decision support tool and highlight results that provide general guidance for biologists and managers. We focused this work on cutthroat trout and brook trout because they represent a widespread and well-defined problem in central and northern Rocky Mountain streams (Fausch et al. 2006), but we believe our approach can be readily adapted to other species.

Materials and methods

Background and conceptual foundation

Cutthroat trout have declined throughout their range in the United States (e.g., Young 1995). There are six major extant subspecies in the Rocky Mountains (Behnke 1992), all of which have either been listed ($n = 3$) or petitioned for listing under the Endangered Species Act. WCT have been proposed for listing, but determined to be not warranted (US Fish and Wildlife Service (USFWS) 2003). That decision remains controversial (Allendorf et al. 2004, 2005; Campton and Kaeding 2005), but it is clear that many populations are at risk (Shepard et al. 2005), and managers are concerned with conservation of both the genetic and ecological integrity of remaining populations. We focus our analysis on WCT because they still inhabit large areas of connected habitat, because we have relatively good information about distributions and habitat use, and because there is considerable debate among biologists about the risks associated with isolation and invasion (Fausch et al. 2006). WCT are thought to occupy more than half of their historical range, with range losses attributed to overexploitation, habitat degradation and fragmentation, and nonnative fish invasions (McIntyre and Rieman 1995; Shepard et al. 2005). Considerable work on habitat use suggests that most spawning and early rearing is in small (≤4th-order) headwater tributaries. Resident individuals may spend their entire life in natal or nearby streams, but migratory individuals that move long distances (10–100 km) are important in many systems (McIntyre and Rieman 1995).

Our approach focused on persistence of WCT associated with individual tributaries or tributary networks representing spawning and early rearing habitat for any life history form. Natal habitat is discontinuous throughout a river basin, so tributaries can be viewed as local populations embedded in a larger metapopulation (Rieman and Dunham 2000; Dunham et al. 2002*b*) if migration and dispersal occur or as solitary isolates if this does not occur. Because brook trout invasion is considered a primary threat to persistence of WCT (and other cutthroat trout) across much of its range (Young 1995; Thurow et al. 1997; Dunham et al. 2002*a*), we developed a framework that considered trade-offs between the potential effects of intentional isolation (to preempt brook trout invasion) and of invasion, both mediated by habitat and environmental conditions. Invasion by rainbow trout is also a threat through hybridization and genetic introgression (Allendorf et al. 2001, 2004), but a formal consideration of genetic threats to WCT was beyond the scope of our primary objective. Although we did not attempt to directly model effects of rainbow trout invasion, our work evaluates the general risk from isolation; this could partially inform barrier considerations where threats of introgression are deemed important.

Fausch et al. (2006) framed the evaluation of isolation versus invasion as a series of questions that defined the trade-offs within individual stream networks and relative priorities among them. We formalized that process with a WCT population persistence model structured as a BBN. The probability of persistence for any local WCT population of interest can be estimated as a function of environmental conditions believed to influence the potential for successful invasion by brook trout, abundance of the resulting brook trout population, abundance and resilience of WCT, and the result of ecological interactions between the two species. Because of fundamental limitations in species persistence or viability models (Ralls et al. 2002), we viewed probabilities of persistence as relative measures useful for comparing alternatives within and among streams. For example, the probabilities could be used to evaluate the effect of a migration barrier on a WCT population and then compare conservation opportunities among a group of populations. The model represents a belief system founded on our collective understanding of WCT and brook trout biology and habitat requirements, but we are also attempting to validate this model with field data in a separate effort.

The model

We developed our BBN following general procedures outlined elsewhere (Cain 2001; Marcot et al. 2006; Marcot 2007). Briefly, we began with a series of meetings among the authors and biologists working with WCT throughout its range. We identified the primary environmental conditions associated with WCT, brook trout, and their ecological interactions. Subsequently, we developed conceptual models (box-and-arrow diagrams) that depicted the hypothesized causal relationships and processes important to these species. The conceptual models were refined through iterative discussion to capture only essential (and quantifiable) relationships in their simplest possible forms.

The final conceptual model (Fig. 1) was converted to a BBN by quantifying the conditional relationships among the attributes and processes represented by the diagram. Each network variable or "node" was described as a set of discrete states that represented possible conditions or values given the node's definition (Table 1). Arrows represent dependence or a cause-and-effect relationship between corresponding nodes. Conditional dependencies among nodes were represented by conditional probability tables (CPTs) that quantify the combined response of each node to its contributing nodes, along with the uncertainty in that response (Supplemental Appendix S1[4]). Input nodes ideally represent proximate attributes of causal influence in the network, such as stream temperature or existence of a barrier, and do not have contributing nodes. The BBN was implemented in the modeling shell Netica (Norsys Software Corp., Vancouver, Brit-

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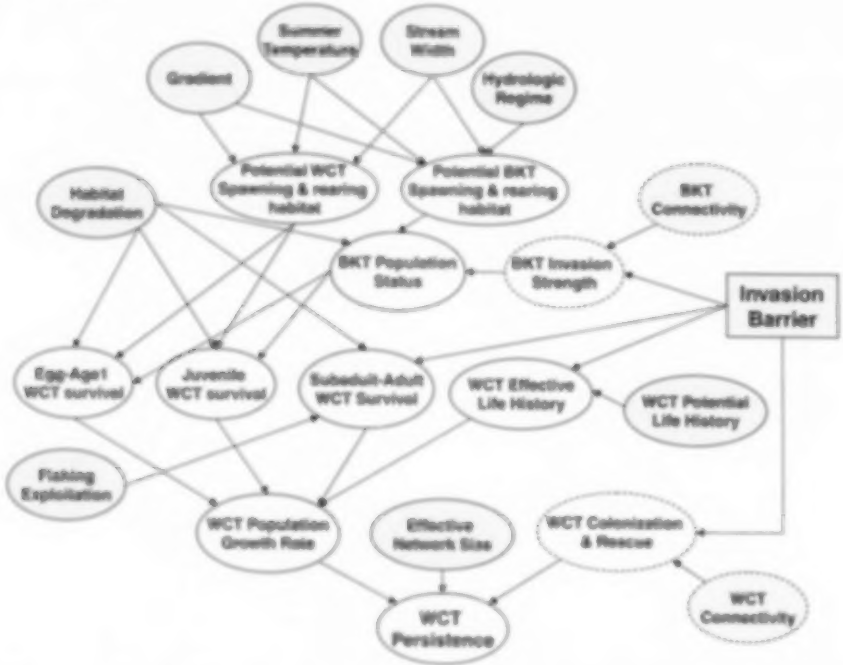
[4] Supplementary data for this article are available on the journal Web site (cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3722. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Fig. 1. Conceptual model depicting environmental conditions and processes influencing persistence of westslope cutthroat trout (WCT, *Oncorhynchus clarkii lewisi*) and the trade-offs between intentional isolation and invasion by brook trout (BKT, *Salvelinus fontinalis*). Shaded ovals indicate input variables or nodes (prior conditions) believed to affect WCT and BKT populations; dashed ovals indicate influences that originate outside the local stream network; the rectangle (invasion barrier) indicates the primary management decision; and arrows indicate conditional relationships among variables (nodes). See Table 1 for node definitions and range of values or categories (states) assigned to each node.


Summer Temperature
Stream Width
Gradient
Hydrologic Regime
Potential WCT Spawning & rearing habitat
Potential BKT Spawning & rearing habitat
Habitat Degradation
BKT Connectivity
BKT Population Status
BKT Invasion Strength
Invasion Barrier
Egg-Age1 WCT survival
Juvenile WCT survival
Subadult-Adult WCT Survival
WCT Effective Life History
WCT Potential Life History
Fishing Exploitation
WCT Population Growth Rate
Effective Network Size
WCT Colonization & Rescue
WCT Connectivity
WCT Persistence

ish Columbia), which uses advanced algorithms to update the probability distributions of all variables in the network given evidence, findings, or presumed initial conditions entered at a variable or subset of variables.

General form of the model

Our final conceptual model (Fig. 1) and BBN included 22 nodes (Table 1; see Supplemental Appendix S1[4] for detailed node definitions and CPTs). The foundation of our approach was in two models of population persistence and demography. First, following Dennis et al. (1991) and application of these methods to threatened salmonid populations (Sabo et al. 2004), we considered the probability of persistence to be a function of population growth rate and population size, which was constrained by the effective network size defining a local population. Persistence also can be influenced by immigration represented through colonization and rescue from nearby populations. In essence, small populations confined to limited areas with highly variable or negative growth rates and little chance for support from surrounding populations will be less likely to persist than those that have stable or positive growth rates, large or complex areas of available habitat, and the potential for frequent demographic support from surrounding populations. Second, the population growth rate for WCT was estimated as a function of stage-specific survival rates (subadult–adult; juvenile; egg–age 1) and the expression of a migratory or resident life history, which defined the expected fecundity of spawning females. This demographic representation of stage-specific survival and reproductive output in the BBN is analagous to a stage-based matrix model commonly used to evaluate population response to changes in vital rates (Kareiva et al. 2000; Caswell 2001). We assumed no density dependence in estimates of population growth rate, primarily because there is little data to model that process for this species. Also, our objective was a model that focused on tradeoffs and priorities among small populations that likely exist at densities below carrying capacity because of other constraints, such as habitat alteration. Although the lack of density dependence may bias our absolute estimates of persistence, others working with similar salmonid populations found this simplifying assumption does not substantially constrain utility of extinction probabilities used to consider relative vulnerabilities (Botsford and Brittnacher 1998; Sabo et al. 2004).

Our primary interest was to model the influence of brook trout invasion and the intentional use of barriers on cutthroat trout persistence. In our model, presence of an invasion barrier could influence persistence of WCT by eliminating migratory life histories and potential for colonization and rescue from surrounding tributaries and by stopping invasion by brook trout. We also assumed that a barrier could reduce survival of older (subadult–adult) WCT that are large enough for extensive movement (e.g., Bjornn and Mallett

Table 1. Node definitions and states for the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN).

Node name[a]	Definition	State
Temperature (I)	Mean summer water temperature over the stream network from 15 July to 15 September	Very low: <7 °C Low: 7–10 °C Optimum: 10–15 °C High: 15–18 °C Very high: >18 °C
Gradient (I)	Mean percent gradient over the stream network	Low: <2% Moderate: 2%–8% High: >8%
Stream width (I)	Mean wetted width over the stream network during base flow	Small: <3 m Medium: 3–10 m Large: >10 m
Hydrologic regime (I)	Seasonal patterns of runoff and flooding that might influence bed scour and subsequent incubation or emergence success of fall spawning salmonids like BKT	Snowmelt Mixed rain-on-snow and snowmelt
Potential spawning and rearing habitat	The potential for successful reproduction and early rearing by WCT based on the physical template for natal habitat as influenced by stream gradient, summer water temperature, and stream size (width)	Low Moderate High
Potential BKT spawning and rearing habitat	The potential for successful reproduction and early rearing by BKT based on the physical template for natal habitat as influenced by stream gradient, summer water temperature, stream size (width), and the dominant hydrologic regime	Low Moderate High
Invasion barrier (I)	A natural or human-constructed barrier that precludes upstream movement by stream fishes	Yes No
BKT connectivity (I)	The potential for invasion by BKT into the local stream network based on the magnitude and frequency of BKT immigration as influenced by the number, distribution, and attributes of potential source BKT populations outside the local stream network and the characteristics of the movement corridor	Strong Moderate None
BKT invasion strength	Realized or effective "BKT connectivity" as influenced by whether or not an invasion barrier is present or will be installed	Strong Moderate None
Habitat degradation (I)	Whether salmonid habitat and the processes that create and maintain it have been altered by human activity	Altered and degraded Minimally altered or pristine
BKT population status	The potential strength of a BKT population in a stream segment as influenced by the realized condition of natal habitat and the likelihood of BKT immigration	Strong Weak Absent
Fishing exploitation (I)	Fishing exploitation rate of subadult and adult (aged 2 and older) WCT in a stream network	Low: <10% annual exploitation High: >10% annual exploitation
Egg to age-1 survival	WCT survival from egg to age 1 as influenced by realized habitat conditions and interactions with nonnative BKT	Low: <2.5% Moderate: 2.5%–5% High: > 5%
Juvenile survival	WCT survival from age 1 to age 2 as influenced by realized habitat conditions and interactions with nonnative BKT	Low: < 25% Moderate: 25%–35% High: >35%
Subadult–adult survival	Annual survival of subadult and adult WCT (ages 2 and older) as influenced by realized habitat conditions, fishing, and presence of an invasion barrier	Low: <35% Moderate: 35%–45% High: >45%

Table 1 (*concluded*).

Node name[a]	Definition	State
Potential life history (I)	The potential expression of migratory and resident life histories for WCT in a stream network; the potential influence of life history expression on the resilience of WCT is assumed to be primarily through the differential reproductive contribution of distinct migratory forms	Resident (low fecundity) Migratory (high fecundity)
Effective life history	Actual life history expression based on a "potential life history" and whether or not an invasion barrier is planned or installed (i.e., migratory life history is lost with installation of barrier)	Resident (low fecundity) Migratory (high fecundity)
Population growth rate	The potential finite rate of population increase (lambda or λ) for the local population of WCT as influenced by reproductive success and recruitment, stage-specific survival rates, and fecundity based on the predominant life history; the node defines population growth potential in the absence of density dependence and environmental variation	Very low: $\lambda < 0.85$ Low: $\lambda = 0.85$–0.95 Moderate: $\lambda = 0.95$–1.05 High: $\lambda = 1.05$–1.15 Very high: $\lambda > 1.15$
Connectivity (I)	The potential for immigration and demographic support for a local population of WCT based on the distribution, interconnection with, and independence of surrounding populations present in other stream networks; it is influenced by the expression of migratory life histories, barriers to movement, and the distribution and characteristics of neighboring populations	None Moderate Strong
Colonization and rescue	Realized or effective connectivity of WCT as influenced by "connectivity" and whether or not an invasion barrier is planned or installed	None Moderate Strong
Effective network size (I)[b]	Size or spatial extent of the local population and its vulnerability to environmental variation and catastrophic events; we use population size (age 1 and older) as our primary metric for the analysis, but assume that population size and network size (km) are directly related	Very small: <3 km or <500 WCT Small: 3–5 km or 500–1000 WCT Moderate: 5–7 km or 1000–2500 WCT Large: 7–10 km or 2500–5000 WCT Very large: >10 km or >5000 WCT
Persistence	The presence of a functionally viable local WCT population for at least 20 years	Absent Present

Note: Nodes that refer specifically to brook trout (BKT, *Salvelinus fontinalis*) population ecology are so noted (e.g., potential BKT spawning and rearing habitat, BKT invasion strength). Nodes without a species designation refer either specifically to westslope cutthroat trout (WCT, *Oncorhynchus clarkii lewisi*) population ecology (e.g., fishing exploitation, potential spawning and rearing habitat, juvenile survival, persistence) or variables with a common influence on both species (e.g., temperature, habitat degradation, etc.). Details regarding definition of the nodes and information used to develop the associated conditional probability tables are in Supplemental Appendix S1[4].

[a] Input nodes (I) are those where the BBN user designates the prior probability of being in a particular state.

[b] "Effective network size" can be expressed as either length (km) of connected spawning and rearing habitat in a local stream network or the population size of individuals age 1 and older (age 1+) within the stream network.

1964; Zurstadt and Stephan 2004), because any fish moving downstream over a barrier will be lost from an isolated population. We assumed brook trout could influence juvenile survival and egg to age-1 survival of WCT directly by competition and (or) predation, but would not influence subadult–adult survival (Peterson et al. 2004).

A suite of other nodes was used to represent the influence of habitat and environmental conditions on these biological processes. Stream channel characteristics (gradient, temperature, and width) are commonly associated with the distribution and abundance of brook trout and WCT and were used here to delimit potential spawning and rearing habitat for both species (Supplemental Appendix S1[4]). Habitat degradation represented departure of habitat quality caused by land management, such as road building, grazing, mining, and timber harvest. Habitat degradation is believed to decrease survival of cutthroat trout and abundance of brook trout and to affect the outcome of ecological interactions between them (e.g., Shepard 2004). Hydrologic regime (timing and magnitude of flow) is hypothesized to have an important influence on population ecology of nonnative salmonids if high flows that scour streambeds coincide with egg incubation and alevin development (e.g., Strange et al. 1992; Fausch et al. 2001). We speculate that the effect of regional hydrologic patterns on reproduction may, in part, explain the variable success of brook trout invasion in some areas

(Fausch et al. 2006). Hydrologic regime was not considered important for WCT because the species presumably has adapted to flow patterns that exist within its native range. Fishing exploitation can reduce survival of WCT (McIntyre and Rieman 1995) and was included as an influence on subadult–adult survival. We did not consider fishing important for brook trout because they are believed to be less vulnerable than cutthroat trout (MacPhee 1966; Paul et al. 2003), and they are rarely targeted in major sport fisheries of this region. Connectivity for brook trout and for WCT represented size and proximity of surrounding tributary populations that could act as sources of invasion (brook trout) and immigration (cutthroat trout, via colonization and rescue). Potential life history represented the dominant life history (migratory or resident) expected in the WCT population, whereas effective life history indicated how life history expression could be constrained by an intentional migration barrier. Migratory life histories in salmonid populations may contribute to resilience and persistence of populations through enhanced growth and fecundity and through facilitation of gene flow and demographic support among tributaries (Rieman and Dunham 2000; Dunham et al. 2003; Neville et al. 2006). Generally, we anticipate tributary populations in large, relatively intact river basins will have an important if not dominant component of migratory individuals (McIntyre and Rieman 1995), but acknowledge that migratory forms may be lost, even when barriers don't exist, because of main-stem habitat degradation or other factors limiting suitability of downstream rearing or migratory habitat.

We did not explicitly represent survival and population growth rates for brook trout as we did for WCT, but rather used brook trout population status as an index of population size. In essence, we tried to predict whether brook trout would be established, and if they were, we assumed that competitive or predatory effects of brook trout would be directly related to the density of the resulting population (i.e., strong populations had a greater effect than weak ones).

Issues of scale

The BBN represented factors influencing a WCT population at several spatial scales. Persistence was considered at the scale of a local population defined by its associated spawning and rearing habitats. This is consistent with the patch concept of Dunham et al. (2002*b*). The spatial extent of the local stream network (effective network size) is ultimately defined by the presence of a barrier or a demographically important discontinuity in habitat, such as a dramatic change in stream size at a tributary junction (e.g., Dunham et al. 2002*b*). The stream channel characteristics (gradient, temperature, and stream width) that define potential spawning and rearing habitat are commonly measured at the scale of individual habitat units and averaged over longer segments of streams. Because a local stream network that defines a population would generally consist of multiple stream segments, there is a potential mismatch in scale between these habitat characteristics and the resulting estimates of WCT persistence. In application of the BBN, we considered a range of values associated with stream channel characteristics representative of the larger stream network. We broadly categorized channel characteristics (see Table 1; Supplemental Appendix S1[4]) to encompass variation among stream segments within many habitat networks. In the case of unusually large stream networks with substantial variation in conditions, the range of variation must be represented in the BBN by the distribution of probabilities reflecting average conditions in that system.

We defined the temporal scale for our BBN as 20 years. We chose this interval because it is difficult to anticipate population trends over much longer periods (Beissinger and Westphal 1998; Ralls et al. 2002). This also is roughly the time scale associated with federal land management planning and with substantial changes in habitat associated with both restoration and degradation. The BBN was not dynamic in the sense that cyclic biological processes are expressed through time steps, as often used in population simulation (Marcot et al. 2001). Rather, time dependence was explicitly considered in the population growth model used to parameterize the BBN (e.g., Lee and Rieman 1997; Shepard et al. 1997). Conditional probabilities in each node reflected our belief about future states once physical and biological processes have played out. In developing the CPTs, we assumed that initial conditions established in the input nodes represented the present, and these factors influenced the outcome (i.e., WCT persistence) expected after 20 years (Supplemental Appendix S1[4]). For example, any population with a negative population growth rate is deterministically fated to extinction if conditions influencing the growth rate do not change and the evaluation is not bounded in time. However, if growth rate is not strongly negative or if the population is initially large, it may well persist for 20 years.

Conditional relationships

The CPTs represent our belief about the probability of a node being in a state given information in the contributing nodes. By default, we used uniform prior probabilities for input nodes during model development and entered specific values during analyses to represent conditions in a watershed or stream network of interest. We crafted CPTs based on published and unpublished data, output from analytical models, expert opinion, and personal experience (Table 1; Supplemental Appendix S1[4]). The relationships between potential natal habitat for both species and channel characteristics (i.e., gradient, temperature, and stream width) were based on field observations and laboratory experiments summarized from the literature and our own work (Supplemental Appendix S1[4]). The CPTs for most other input nodes relied largely on a synthesis of existing theory and empirical observation (see Fausch et al. 2006 for an overview). For example, the CPT that represents how potential spawning and rearing habitat, habitat degradation, and brook trout population strength affect egg to age-1 survival of WCT was derived from our observations and discussion in the context of available work on these and similar species (Table 2; Supplemental Appendix S1[4]). Lack of detailed information on key processes that influence invasion dynamics and species interactions led us to draw on a variety of information types (e.g., data, opinion, experience) to specify conditional relationships. The CPTs for most nodes where opinion was required were developed by two or more authors independently, but after full discussion and review of available infor-

Table 2. Conditional probability table (CPT) for egg to age-1 survival of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) as an example of the conditional relationships underlying connected nodes in the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN).

Contributing (parent) nodes			Probability of a given state for survival		
Brook trout population status	Potential spawning and rearing habitat	Habitat degradation	Low	Moderate	High
Strong	Low	Degraded	1.00	0	0
		Minimally altered	1.00	0	0
	Moderate	Degraded	1.00	0	0
		Minimally altered	0.90	0.10	0
	High	Degraded	0.95	0.05	0
		Minimally altered	0.75	0.25	0
Weak	Low	Degraded	0.85	0.15	0
		Minimally altered	0.75	0.25	0
	Moderate	Degraded	0.65	0.35	0
		Minimally altered	0.50	0.50	0
	High	Degraded	0.45	0.45	0.10
		Minimally altered	0.20	0.55	0.25
Absent	Low	Degraded	0.75	0.25	0
		Minimally altered	0.45	0.50	0.05
	Moderate	Degraded	0.15	0.60	0.25
		Minimally altered	0	0.50	0.50
	High	Degraded	0.05	0.40	0.55
		Minimally altered	0	0	1.00

Note: This CPT was populated by expert opinion based on the probabilities averaged across the five co-authors.

mation. Where consensus for a CPT was not achieved, we accounted for uncertainty arising from differences of opinion among us by averaging the conditional probabilities among possible outcomes to arrive at a final CPT. More generally, the distribution of probabilities for any CPT represented uncertainty about the ecological processes depicted in the BBN as well as the expected variability in the response or outcome (e.g., Table 2).

The CPTs for population growth rate and persistence were developed using output from the two population models described earlier. We estimated conditional probabilities associated with potential population growth rate based on 1000 replicate simulations of a stage-based matrix model using vital rates drawn randomly from distributions representing the range of conditions possible in the parent nodes (e.g., stage-specific survival and fecundity associated with effective life history; Supplemental Appendix S1[4]). Simulations were implemented by spreadsheet using a Monte Carlo procedure and population analysis module developed for Excel (Hood 2004). Variation in output among replicates for a set of initial conditions represented uncertainty in vital rate estimates rather than environmental or demographic stochasticity (Supplemental Appendix S1[4]). We estimated the probability of persistence using the method of Dennis et al. (1991) based on our estimates of population growth rate, variance in that growth rate, initial population size, and the 20-year time horizon. Growth rate and initial population size could be inferred directly from the contributing (parent) nodes (Fig. 1). We used the analytical method to estimate persistence rather than a stochastic simulation with the matrix model because we have no information to guide estimates of the environmentally forced variances associated with each vital rate. We do, however, have estimates of the range in variances associated with population growth rates for WCT (e.g., McIntyre and Rieman 1995) and assumed that this variance was inversely related to population size (e.g., Rieman and McIntyre 1993). We refer to the completed BBN as InvAD (isolation and invasion analysis and decision) or the InvAD BBN.

To consider the importance of uncertainty in our assumptions about the conditional relationships for population growth rate and persistence, we developed three alternative BBNs that were identical conceptually to the InvAD BBN (i.e., having the same box-and-arrow diagrams as Fig. 1) but with different CPTs (Supplemental Appendix S1[4]). The first two alternates had CPTs for persistence where the variance in population growth rate was either assumed to be independent of population size with a constant value of 0.2 (low constant variance) or to be independent of population size with a value of 0.8 (high constant variance). To determine if expert judgment strongly deviated from the output of the two demographic models, we developed a third alternative where the CPTs for population growth rate and persistence were both based on opinion as informed by empirical data and professional experience (opinion only). We subsequently compared the performance of these alternative models with the InvAD BBN. We concluded that predictions were generally consistent (Supplemental Appendix S2[4]), so we only present analyses and results from the original model.

Analyses

To characterize the behavior of the InvAD BBN, we conducted two analyses under a standard set of conditions. First, to understand how predictions were influenced by a particular environmental or biological condition, we conducted general sensitivity analyses assuming no prior knowledge about

Table 3. Variables representing standard environmental conditions and inputs manipulated under the hypothetical example to explore trade-offs between invasion and isolation of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) threatened by brook trout (*Salvelinus fontinalis*).

Node	State
Standard variables	
Gradient	<2%
Stream width	<3 m
Temperature	10–15 °C
Hydrologic regime	Snowmelt
Brook trout connectivity	Strong
Manipulated variables	
Invasion barrier	Yes, no
Potential life history	Migratory, resident
Connectivity	High, none
Habitat degradation	Yes, no
Fishing exploitation	High, low
Effective network size	Very small, medium, very large

Note: The isolation and invasion analysis and decision Bayesian belief network (InvAD BBN) was used to generate estimates for westslope cutthroat trout persistence for 48 different scenarios based on the state combinations of the manipulated variables. The standard conditions were selected so that habitat was equally suitable for both species.

states of input nodes (i.e., uniform prior probabilities or complete uncertainty) by estimating entropy reduction values (i.e., based on mutual information formulae in Pearl (1991) and implemented in Netica) for all nodes and by changing the initial conditions of input nodes and plotting the range of predicted responses. Second, to assess the relative changes in persistence from barriers and other management options, we generated a series of predictions for 48 scenarios using a standard set of initial conditions typical of WCT streams in the northern Rocky Mountains while manipulating a subset of input conditions that might vary in response to management history or population characteristics (Table 3).

To explore application of the model in real-world management, we used the InvAD BBN to predict WCT persistence in three streams in the northern Rocky Mountains within the Lolo National Forest in western Montana, where conservation efforts focus on WCT and where brook trout were a known threat. These examples focused on changes in persistence (from current conditions) relative to barrier construction or removal and other management options. The Lolo National Forest is roughly situated at the geographic center of WCT's historical range in the United States (Shepard et al. 2005). WCT populations in the region occupy both isolated tributary streams and larger interconnected stream systems (Shepard et al. 2005). For each scenario we analyzed, fishery biologists from Lolo National Forest were asked to describe the invasion threat from brook trout and existing or proposed migration barriers, define environmental and physical conditions required as BBN inputs, and provide any additional contextual information relevant to the biology of WCT (e.g., presence of other nonnative fish species). The model was used to generate predictions and explore alternative management actions based on the site-specific information.

Results

Sensitivity analyses and model behavior

Sensitivity analyses indicated that the BBN generally behaved as we intended based on its structure and the relative influences of the variables we believed were important. Population size (or extent of habitat) and demographic characteristics strongly affect predicted probability of persistence. Entropy reduction estimates considering all 21 variables indicated that predictions of persistence were two–three times more sensitive to information about population growth rate (0.188) than the next most influential variables: effective network size (0.092) and subadult–adult survival (0.054) (Table 4). Results generally reflected a proximity effect, where the influence of a particular node is inversely related to the number of intervening links (Fig. 1, Table 4). In one exception, persistence was more sensitive to one of its grandparents (subadult–adult survival) than to one of its parents (colonization and rescue).

Among input variables only, both analytical (Table 4) and graphical representations (Fig. 2) demonstrated that effective network size was most influential. Four of the seven most important nodes either represent or directly influence habitat connectivity, migration, and dispersal (e.g., potential life history, invasion barrier, connectivity, BKT connectivity; Fig. 2). However, their relative effect was, on average, about one-third that of effective network size (e.g., compare width of bars in Fig. 2).

Relative effect of isolation management on persistence

In the generalized examples that explored isolation management in response to brook trout invasion threats across a range of initial conditions (Table 3), the relative influence of invasion barriers depended strongly on effective network size, habitat conditions in the network, and potential expression of migratory life histories (Fig. 3). The probability of persistence of a local WCT population increased as the effective network size increased (Fig. 3). This pattern was consistent across all combinations of variables in the examples, including installation of a migration barrier. A barrier always increased the probability of persistence for a population with no migratory component or no potential for immigrants from other WCT populations. In contrast, a barrier almost always reduced the probability of persistence when the existing population expressed a migratory life history and was strongly connected to other populations.

Although direction of change in persistence with a barrier depended consistently on life history and connectivity, the magnitude of change depended on other conditions as well. Habitat degradation and fishing, for example, tended to increase risk for migratory, connected populations beyond that resulting from barrier installation and to reduce the relative benefits of intentional isolation for a resident, nonmigratory population threatened by invasion. Habitat degradation had a similar influence and was more important than fishing averaged across other factors (Fig. 3).

Case studies: intentional isolation and other management options in three streams

The range of conditions in the three streams from Lolo National Forest allowed us to explore the nature of trade-offs

Table 4. Sensitivity of predicted persistence for westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) to all contributing nodes in the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN) relative to the number of intervening links.

Node	No. of links to persistence[a]	Sensitivity[b]
Population growth rate	1	0.188
Effective network size	1	0.092
Subadult–adult survival	2	0.054
Effective life history	2	0.043
Egg to age-1 survival	2	0.031
Invasion barrier	2–5	0.025
Colonization and rescue	1	0.023
Juvenile survival	2	0.020
Habitat degradation	3–4	0.016
Fishing exploitation	3	0.014
Potential spawning and rearing habitat	3	0.012
Potential life history	3	0.011
Brook trout invasion strength	4	0.007
Temperature	4–5	0.003
Connectivity	2	0.002
Brook trout population status	3	0.002
Stream width	4–5	0.002
Brook trout connectivity	5	0.001
Potential brook trout spawning and rearing habitat	4	<0.001
Gradient	4–5	<0.001
Hydrologic regime	5	<0.001

Note: Survival and population growth rate nodes refer to westslope cutthroat trout.

[a] A value of 1 indicates a direct connection between nodes. Some nodes have a range of links because they affect more than one variable in the Bayesian belief network (BBN); thus their effect can cascade through the network by different paths.

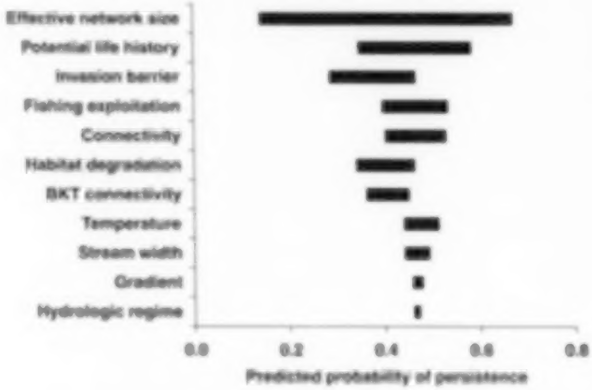
[b] Sensitivity values (entropy reduction) assumed a uniform prior probability distribution for each of the 11 input nodes and were calculated in Netica using the mutual information formula that appears in Pearl (1991, p. 321) that is implemented in Netica (B. Boerlange, Norsys Software Corporation, 3512 West 23rd Avenue, Vancouver, BC V6S 1K5, personal communication). Marcot et al. (2006) present the same formula. Values integrate the influence of nodes having a range of links.

biologists and managers might encounter when trying to assess what could be achieved through installation or removal of barriers relative to other management actions (Fig. 4, Tables 5 and 6).

Silver Creek

Silver Creek contains a genetically pure WCT population isolated above a culvert in a large stream network (>10 km) (Fig. 4). Invasion by brook trout that occur immediately downstream was considered imminent without a barrier. Potential management actions were to remove the existing culvert barrier (and replace with a bridge or passable culvert), thereby reconnecting the isolated population to populations in adjacent stream networks and downstream habitats, or to modify or replace the barrier with a structure that can withstand extreme environmental conditions (e.g., floods) and ensure continued isolation. The probability of persistence was predicted to increase from 0.81 to 0.97 if the existing barrier was removed. The apparent benefit resulted from the expectation that the existing population would re-express a migratory life history and connection with other populations in the Saint Regis River system. The relative increase was modest because the existing isolated network was already relatively large and habitat was good. The analysis suggested that the local population was likely to persist with or without a barrier. If maintenance of genetic purity were a priority, then intentional isolation would also preclude invasion by rainbow trout and WCT × rainbow trout hybrids.

Fig. 2. Sensitivity of persistence to input nodes in the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN). Values were generated by sequentially manipulating the state probabilities of each input node to produce the lowest and highest predicted values for persistence while maintaining uniform prior probabilities for all the other input nodes (except invasion barrier). Invasion barrier was set to "no" for all input variables to represent a default condition. The value for invasion barrier represents sensitivity to the management decision under complete uncertainty about the most likely state of other inputs. Unless otherwise noted, nodes refer to westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) or environmental conditions common to both species. BKT, brook trout (*Salvelinus fontinalis*).

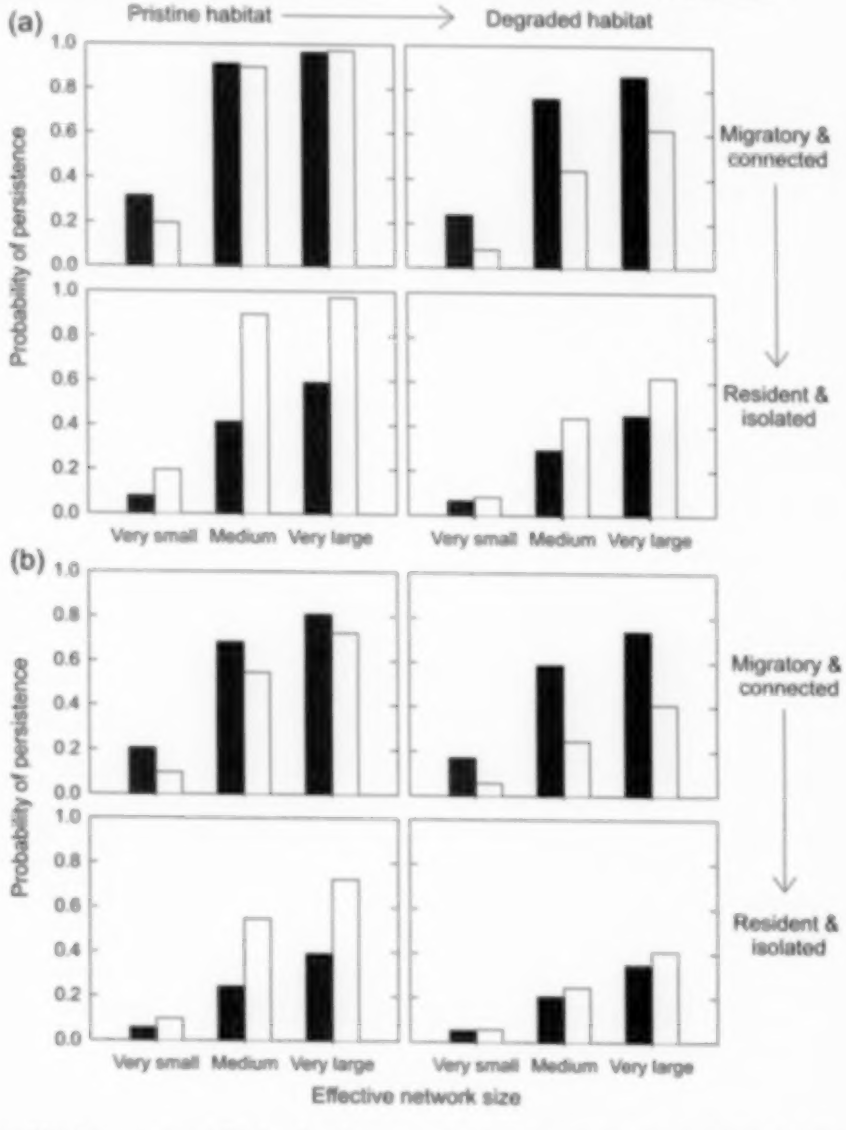


Dominion Creek

Dominion Creek contains a WCT population believed to be genetically pure and fragmented by two culvert barriers (Fig. 4). There was a total of approximately 4.25 km of suitable habitat between the lower (near the stream's mouth) and upper barrier (1.5 km) and above the upper barrier (2.75 km). Brook trout are already established between the lower and upper barriers. Potential management actions were to (1) remove the upper barrier to increase the effective network size for the WCT population above the lower barrier, (2) remove the lower barrier to connect the lower population fragment to other stream networks, (3) remove both barriers, (4) eradicate brook trout between the two barriers, and (5) eradicate brook trout and remove the upper barrier (i.e., actions 1 and 4).

Under existing conditions in Dominion Creek, the estimated persistence in the lower (brook trout established) and upper (brook trout absent) stream segments was 0.11 and 0.22, respectively. Removing the upper barrier increased the

Fig. 3. Predicted response of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) to installation of an invasion barrier based on the management scenarios described in Table 3 and using the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN). Bars denote the predicted probability of persistence with (open bars) or without (solid bars) a barrier relative to habitat size and quality, life history expression, connection to other populations, and low (*a*) or high (*b*) fishing exploitation.



estimate for the combined segment to 0.38, but brook trout are then expected to become established throughout the stream. Removing the lower barrier increased the estimate for the lower segment to 0.37, but the largest relative benefit was expected through removing both barriers (estimated persistence = 0.86). The eradication of brook trout in the lower segment increased estimated WCT persistence from 0.11 to 0.22, whereas eradication plus removal of the upper barrier substantially decreased risk (i.e., estimated persistence = 0.75).

Intentional isolation with two barriers did not appear to be a highly effective alternative in Dominion Creek. The single-barrier option offered substantial benefit only if implemented in conjunction with brook trout eradication. The cost and effort required to attempt eradication can be substantial (Shepard et al. 2002) and the ultimate success uncertain (Meyer et al. 2006), but the combination of brook trout removal and isolation (which would also preempt introgression with rainbow trout) might be considered if the WCT population was considered an unusually important contribution to total genetic diversity for the species (Fausch et al. 2006). If the Dominion Creek population does not represent an important element of genetic diversity and (or) brook trout eradication is not feasible, then conservation ef-

Fig. 4. General location and orientation of three streams (*a*–*c*) in Lolo National Forest (shaded area in inset) used for the case study analysis. Streams contain populations of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) threatened with invasion by brook trout (*Salvelinus fontinalis*). Circles indicate locations of existing fish migration barriers; darker lines denote the main stem, and arrows show the direction of stream flow.

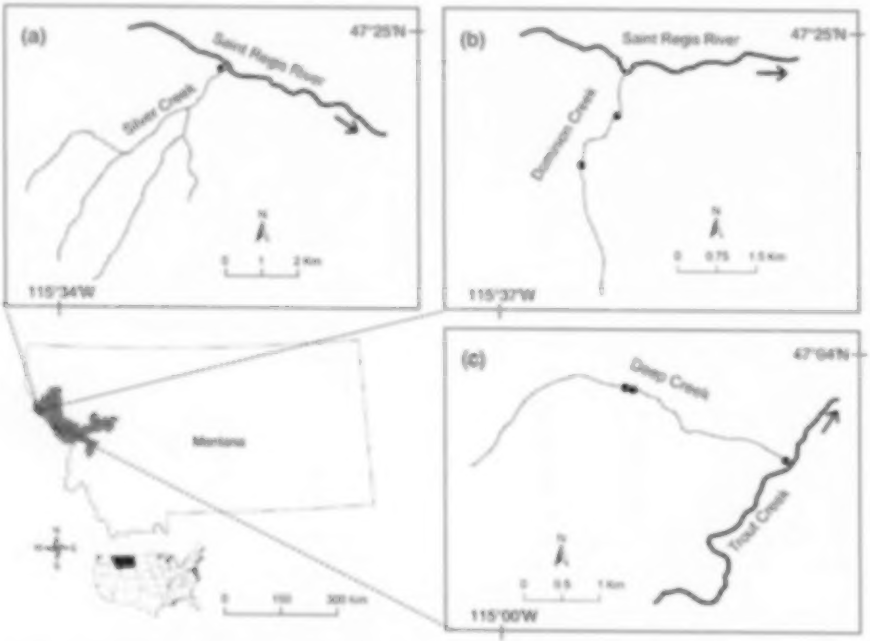


Table 5. Existing conditions for three westslope cutthroat trout (WCT, *Oncorhynchus clarkii lewisi*) streams in Lolo National Forest that are threatened by invasion from nonnative brook trout (*Salvelinus fontinalis*) and possible management actions involving barrier maintenance or removal and habitat restoration that were analyzed using the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN).

	State of node or existing condition[a]		
Node or factor affecting WCT persistence	Silver Creek	Dominion Creek	Deep Creek
Gradient	2%–8%	2%–8%	2%–8%
Temperature	7–10 °C, 10–15 °C	10–15 °C	10–15 °C
Stream width	3–10 m	<3 m	<3 m
Hydrologic regime	Mixed	Snowmelt	Snowmelt
Habitat degradation	Pristine	Pristine	Degraded
Potential life history	Migratory	Migratory	Migratory
(Potential) connectivity	Strong	Strong	Strong
Effective network size	>10 km	<3 km	<3 km
Brook trout connectivity	Moderate	Strong	Strong
Additional nonnative trout threats	RBT, WCT × RBT hybrids	WCT × RBT hybrids	—
No. of existing barriers	1	2	3

Note: Information on streams elicited from B. Riggers and S. Hendrickson, Lolo National Forest, Fort Missoula Building 24, Missoula, MT 59804, USA (August 2006, personal communication).

[a] The probabilities were 1.0 for referenced state in each input node with the exception of temperature in Silver Creek, which was split (0.5, 0.5) between two states. Rainbow trout (RBT, *Oncorhynchus mykiss*) and (or) WCT × RBT hybrids are present below, or in the larger stream below, the downstream barrier in both Silver and Dominion creeks.

forts might be better served by focusing efforts in other larger tributary systems (e.g., Silver Creek).

Deep Creek

Deep Creek contains a WCT population fragmented by a series of three culverts (Fig. 4). Approximately 4.1 km of suitable WCT habitat was collectively distributed between lower (near the stream's mouth) and middle barriers (2.4 km), between the middle and upper barrier (0.1 km), and above the upper barrier (1.6 km). The habitat has been affected by land use and was classified as degraded. Cutthroat trout were not present above the upper barrier. Brook trout were a known invasion threat. Potential management actions were to (1) remove the lower barrier to connect the lower habitat fragment to other stream networks; (2) remove the middle and upper barriers to increase the effective network size isolated by the lower barrier; (3) remove all three barriers to both reconnect the fragmented populations and increase the effective network size; and (4) implement general habitat restoration efforts either in conjunction with barrier removals (1–3 above) or instead of barrier removals.

In Deep Creek, management actions involving both barriers and habitat restoration could be important. Any combination of barrier removal was estimated to increase the probability of persistence for the existing population (Table 6), though there are important differences among them. Removal of all three barriers was estimated to increase the probability of persistence from 0.09 to 0.72 by the combined effect of increasing the network size (from <3 to 3–5 km) and reestablishing the migratory pathway to the larger system (Table 6). The benefits of reconnection appeared to be substantial, whereas removal of the middle and upper barriers provided some benefit, but the risks appeared to remain high (i.e., probability of persistence = 0.30). Removal of the two upper barriers in conjunction with habitat restoration over 4 km of stream could approach the benefit expected with removal of all three barriers (Table 6).

It appears that considerable expense of either removing all barriers or coupling the removal of two barriers with habitat restoration will be required to substantially reduce the risks in Deep Creek. Alternatively, managers could forgo work in this stream and allocate resources to another system where greater benefits might be realized at lower cost.

Discussion

Conservation strategies for inland cutthroat trout including WCT often advocate a combination of efforts to either isolate or reconnect populations to reduce threats from nonnative trout or isolation, respectively (Lentsch et al. 2000; May et al. 2003; Shepard et al. 2005). An objective analysis of the issues and opportunities for either action, however, can be a challenge. We found that development and application of a BBN could help explore the trade-offs between intentional isolation and invasion for WCT populations threatened by invasion. It also provides a foundation for further work in both management and research.

General guidance and further work

The assumptions inherent in the BBN and subsequent analyses suggest two generalizations for management of barriers and invasions. First, a barrier will be more likely to increase the probability of persistence for a WCT population as the expression of migratory life histories becomes limited, demographic links to other populations are reduced, and invasion by brook trout becomes more likely. The relative benefits associated with any barrier, however, can depend primarily on habitat quality and size of the isolated stream network and secondarily on other environmental effects. These general results follow from our understanding of stream salmonid biology (see review by Fausch et al. 2006 and references therein), and the behavior of the model supports the perspective of many biologists that intentional isolation can be an important tool, but with limitations.

Table 6. Estimated probability of persistence for westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) in Deep Creek, Lolo National Forest, under four alternative management actions analyzed using the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN).

		Estimated probability of persistence	
		Habitat improvement	
Barrier removals	Nonnative trout invasion possible	No	Yes
None	No	0.09	0.22
Lower	Yes	0.30	0.38
Middle and upper	No	0.30	0.73
All three	Yes	0.72	0.86

Note: Predictions considered removal of existing barriers, alone and in combination, with and without habitat improvement.

Many WCT populations, especially those east of the Continental Divide in Montana, are functionally and demographically isolated by habitat degradation, dewatering, and loss of downstream rearing habitats (e.g., Shepard et al. 2005) even though a permanent migration barrier may not exist. Other inland cutthroat trout face similar situations (e.g., May et al. 2003; Hirsch et al. 2006; Pritchard and Cowley 2006). Intentional migration barriers could be important tools to reduce any additional threat of invasion in these systems, but priorities might favor isolation of the largest populations and best habitats. For example, continued isolation of Silver Creek could provide an excellent opportunity to conserve a WCT population threatened by brook trout invasion because the existing barrier isolates >10 km of stream habitat, and the processes that create and maintain aquatic habitats in that watershed are intact. In contrast, Deep Creek would require both removal of multiple barriers and habitat restoration (and thus much greater cost) to achieve a comparable result.

Second, maintenance or restoration of fish passage appears to most strongly influence persistence of WCT when the full expression of life histories and strong connection with other populations are anticipated, even if brook trout are expected to invade. In essence, more robust and resilient WCT populations were believed likely to resist displacement by brook trout (i.e., biotic resistance). The relative benefit of maintaining or restoring passage again was dependent principally on the size and quality of the available habitat. Our general results imply that WCT should resist brook trout invasion in the right circumstances.

Results also reflect our assumptions about migratory life histories in WCT and their association with higher individual and population growth rates (Rieman and Apperson 1989), demographic resilience, and connectivity among populations (Rieman and Clayton 1997; Dunham and Rieman 1999; Ayllon et al. 2006). These advantages are consistent with faster growth, larger body size, higher female fecundity, and higher propensity for dispersal among populations that presumably will help WCT resist brook trout invasions or increase their resilience to disturbances (Fausch et al. 2006). Our assumptions and results are consistent with current understanding of demographic process. As yet, however, there is limited empirical evidence that connected, migratory WCT populations actually do better resist invasion, so further investigation is needed to reveal any patterns and characterize the proximate mechanisms (Fausch et al. 2006). We also assumed that isolated WCT populations can fully re-express migratory life histories if connection is restored, but we have little empirical evidence to gauge how quickly this might occur (but see Thrower et al. 2004; Olsen et al. 2006). In the interim, managers might exercise caution and view the benefits of reconnection as a topic for exploration through adaptive management. In some cases, for example, managers have multiple opportunities to maintain or remove barriers. When uncertainty is high, experimentation and monitoring (i.e., remove some barriers, retain others, and monitor the response) could be the most efficient way forward (Fausch et al. 2006).

The BBN and analyses also rest heavily on the assumption that habitat area or population size, particularly for very small tributary systems, will have an important influence on persistence of isolated populations. There are many examples of WCT persisting above barriers (Shepard et al. 2005), but virtually no information on those populations that have disappeared, so our assumptions are based largely on the observations and results with similar species (e.g., Morita and Yamamoto 2002; Fausch et al. 2006). An empirical evaluation of the minimum habitat area (patch size) that will sustain isolated WCT populations for a given period of time would help biologists identify populations at high risk of extirpation from so-called isolation effects such as demographic, genetic, and environmental uncertainty (Caughley 1994). Limited data for other salmonids suggest that patch size–persistence relationships could be species-specific (e.g., Rieman and McIntyre 1995; Dunham et al. 2002*b*; Morita and Yamamoto 2002). Many WCT populations are now isolated by artificial (e.g., culvert) or natural barriers with a known time of construction or formation. An inventory of existing isolates could provide a simple test of the effects of isolation and extinction risk analogous to the work of Morita and Yamamoto (2002) with white-spotted char (*Salvelinus leucomaenis*). Such information could directly extend the utility of the models developed here.

Lessons from BBN development and application

The process of building and applying the BBN to the invasion–isolation issue was useful because it forced both the developers and users to think in greater detail about fundamental mechanisms and processes, ecological context, the logic and conservation values involved in the decision process, and other possible management actions that might complement barriers.

First, the model-building exercise forced us to explicitly define the links between habitat conditions and brook trout and how these factors interact with migration barriers to affect WCT demography. For example, the iterative process of describing key variables and their influences (e.g., Jensen 1996; Cain 2001; Marcot et al. 2006) led us to formally define stage-specific mortality for WCT. In doing so, we partitioned the effect of brook trout invasion within the early life stages of WCT. Following that, we realized we also needed to represent the effect of an invasion barrier on mortality of adult WCT through disruption of nonreproductive movements. The general approach led us to consider the complexity of the barrier–invasion interactions that we might not have anticipated otherwise.

Accounting for these effects in model structure also made it easier to see the detail in intermediate responses, which provided insight into how a particular set of conditions affect risk to WCT populations. For example, use of the InvAD BBN helped visualize how installation of a barrier was predicted to affect survival rates of WCT at different life stages and whether these changes would interact with or potentially compensate for the effect of losing a migratory life history in their influence on the population growth rate (intermediate response). In turn, changes in population growth rate interacted with the loss of connection to other WCT populations to determine the probability that WCT will ultimately persist in the local stream network.

Second, use of a model like the InvAD BBN in a decision process forces the user to evaluate their assumptions and to clearly define the conservation priorities motivating a management choice. USDA Forest Service biologists working through the exercise of critiquing and using the model have routinely commented that the model structure helped them think about all the important processes, not just those they may have emphasized in the past. A broader consideration of ecological process in the context of personal experience can promote communication among biologists that work in different systems or have different professional backgrounds and between research and management. The case study from Deep Creek revealed that some biologists were more optimistic about the resilience of isolated, allopatric WCT populations in a degraded watershed than predicted by the model. The discrepancy initiated a discussion about whether the difference resulted from a relatively imprecise definition of degraded habitat or a possible context dependency in the effect of habitat quality on isolation. Further investigation may be needed to address either possibility, but application of the BBN can initiate the discussion.

Perhaps more importantly, the InvAD BBN compels users to define the conservation priorities underlying a particular decision and how those values relate to the overall conservation strategy. An initial step in a manager's decision process may be to describe conservation values for populations of interest in terms of evolutionary, ecological, and socio-economic characteristics (e.g., Fausch et al. 2006). If, for example, a manager is willing to accept an increased risk through intentional isolation, then he or she must explain that the most important conservation value is the maintenance of an evolutionary legacy (e.g., an irreplaceable component of species' genetic diversity). It follows then that ecological function (connectivity and multiple life history expression) and socio-economic concerns (recreational fishing) either are irrelevant because these characteristics do not exist, or they are secondary concerns. A clear statement of management objectives is particularly important where individual WCT populations face multiple nonnative threats and where these threats vary across a group of populations (e.g., Silver and Deep creeks) managed under a common framework. Our model was not designed to quantify the threat of hybridization, but if a manager placed greater emphasis on the genetic integrity of a WCT population and perceived hybridization as a major threat, then he or she could still explore the relative risk of isolation that came from an interest in avoiding introgression.

This exercise naturally leads to a series of questions that should sharpen the decision process: What are you hoping to conserve? Is the proposed action worth it? What is the relative benefit of taking action with this population versus another? Overall, the model induces biologists and managers to clearly describe the assumptions, logic, and values leading to a decision, which fosters communication (e.g., Steventon et al. 2006).

Caveats

The InvAD BBN is a belief system based on current understanding of brook trout invasion processes and effects and the consequences of incidental or intentional isolation for WCT; potential users should be aware of its limitations. Predictions should be interpreted in terms of the relative differences between management options for a set of environmental conditions, not as absolute probabilities (e.g., Ralls et al. 2002). A BBN provides guidance during the decision process, but does not supplant or replace a human decision (Marcot 2006) nor does it substitute for the professional knowledge of an experienced fishery biologist. It does, however, allow biologists and managers to more clearly think about the relative effects of brook trout and isolation on WCT populations and to quickly visualize and evaluate the effects of complex interactions. As a working hypothesis, it can be directly tested, updated, or modified using examples from fishery management or challenged and revised based on new empirical or theoretical results. Though beyond the scope of the current effort, the model could also be extended to explicitly represent the cost and benefit of particular decisions by adding utility nodes that, for example, depict the financial cost of barrier management or the value derived from increasing the representation of a desired WCT population characteristic such as genetic purity, life history variation, or large body size.

BBNs are relatively straightforward to understand and use, but developing one may be a lengthy, iterative process. We found that a lack of empirical information about certain ecological processes led to extensive debate about which variables to include in the model. Moreover, justifying these variables and their conditional relationships became a major endeavor.

The InvAD BBN was developed to characterize threats to WCT from brook trout and the risk of losing a local population of WCT, but analogous models could be developed to address similar threats to other native species like threatened bull trout (*Salvelinus confluentus*) and to consider effects of multiple invaders or other threats. For example, introgression with rainbow trout (or rainbow trout × cutthroat trout hybrids) is a recognized threat to WCT (e.g., Allendorf et al. 2001, 2004; Shepard et al. 2005) and was a contextual consideration in two of our case study examples. The considerable variation in patterns of introgressive hybridization observed for WCT in some cases (Weigel et al. 2003; Ostberg and Rodriguez 2006) may belie a conservative, simplifying assumption that hybridization will ultimately occur wherever rainbow trout invasion is possible (e.g., Hitt et al. 2003). We caution that although InvAD BBN can quantify the relative risk of isolation that follows from an interest in preventing invasion by nonnative salmonids, the model neither formally considers nor quantifies the threat of hybridization. A synthesis of WCT hybridization dynamics across environmental gradients, for example, would be the first step to an extension that formally quantified such a threat.

The InvAD BBN obviously does not solve the often opposing problems of brook trout invasion and habitat fragmentation facing WCT or other native fishes in western North America. Rather, it provides a process and framework for thinking through the issues, clearly documenting and defining knowledge and uncertainty, and identifying conservation values and objectives. Site-specific analysis using the InvAD BBN or similar BBNs may help identify management options and trade-offs in a particular stream. The greater utility, however, may be using the model to explore the relative benefits of isolation or connection across a collection of WCT populations and using that information to implement more strategic conservation programs and prioritize limited resources.

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Krill diel vertical migration fine dynamics, nocturnal overturns, and their roles for aggregation in stratified flows

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Abstract: A set of high-resolution observations on short-term dynamics of krill diel vertical migrations (DVM) in the St. Lawrence Estuary are presented here, including vertical mass transfer measurements from multifrequency echosounding coupled with stratified net sampling and tracers of individual vertical movements from stomach pigments over a 72 h period. The data set is supplemented by vertical migration speeds and biomass diel patterns from ADCP (acoustic Doppler current profiler) time series lasting up to 3 months. All krill always rapidly migrated to the surface in synchrony at sunset. Soon after the ascent, fed krill started to swim downward. A scattering layer was then formed at their daytime depth with sometimes a significant backscatter at intermediate depths, especially around midnight. A reorganisation in the upper water column then occurs, likely for a predawn feeding bout. At dawn, the krill mass still feeding in upper water column synchronously swam downward to their daytime depth. This nocturnal asynchronous vertical behaviour, conforming to the DVM hunger-satiation hypothesis, repeated between August and October in two different years, the DVM timing being determined by day length.

Résumé : Un ensemble d'observations à haute résolution de la dynamique à court terme des migrations verticales nycthémérales (MVN) du krill dans l'estuaire du Saint-Laurent est présenté. Il incorpore des mesures de transfert de masse sur la verticale à partir d'échosondages multifréquences couplés à l'échantillonnage des strates au filet à nappe et le suivi des mouvements verticaux individuels par des mesures de pigments stomacaux sur une période de 72 h. Des séries temporelles des patrons circadiens des vitesses verticales de migrations déterminées à l'aide d'un ADCP (« acoustic Doppler current profiler »; profileur de courant acoustique à effet Doppler) complètent les mésures sur une période allant jusqu'à 3 mois. L'ensemble du krill migre toujours rapidement et en synchronie jusqu'en surface lors du coucher du soleil. Peu de temps après l'ascension, du krill nourri commence à nager vers le bas, ce qui se poursuit avec une intensité notable jusqu'au milieu de la nuit. Il forme alors une couche acoustique de rétrodiffusion à sa profondeur diurne, ce qui engendre une distribution verticale nocturne bimodale, souvent accompagnée de densités acoustiques notables aux profondeurs intermédiaires, particulièrement au milieu de la nuit. Une réorganisation dans la partie supérieure de la colonne d'eau survient ensuite, vraisemblablement pour une dernière période d'alimentation avant l'aube. A l'aube, la masse de krill s'alimentant toujours dans la partie supérieure de la colonne d'eau nage en synchronie vers sa profondeur diurne. Ce comportement vertical nocturne asynchrone, conforme à l'hypothèse de faim-satiété de la MVN, s'est répété entre les mois d'août et d'octobre à deux années différentes, la synchronisation de la MVN dépendant de la durée du jour.

Introduction

In his review of diel vertical migrations (DVM), Pearre (2003*a*) points out that detecting vertical migrations requires tracking not only mass transfer on the vertical with a temporal resolution that is high enough to adequately cover the diel changes and the fine nocturnal processes, such as the so-called midnight sinking or dawn rise, but also the interchanges of individuals. Under the hunger–satiation hypothesis of Pearre (2003*a*), the DVM is asynchronous within the population: animals leave the surface waters during the night as soon as they are satiated and may go back for a second meal before dawn after digesting their early-night meal (e.g., Simard et al. 1985). Such behaviour often results in bimodal

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vertical distributions during the night (Pearre 1979). Patchiness and advection are additional constraints adding variability that complicates proper in situ detection. Understanding this DVM fine dynamics is not only a relevant academic question of ecosystem dynamics, but also fundamental for comprehensive understanding of mesoscale dispersion and organisation of the biomass under the vertically structured currents in the ocean, namely for the formation and maintenance of aggregations in particular areas that are sought by predators, such as baleen whale feeding grounds.

Three-dimensional (3D) circulation at tidal and other frequencies interacting with abrupt bathymetric features combined with the behaviour of zooplankton on the vertical are key players in aggregation processes (Genin et al. 1994; Mackas et al. 1997; Genin 2004). This is especially evident in stratified dynamic environments and flows such as estuaries (Kimmerer and McKinnon 1987; Roman et al. 2005). Simard et al. (1986*a*) and Runge and Simard (1990) attributed krill aggregation at the head of the St. Lawrence Estuary to the interaction between the deep-flow import of the strong two-layer estuarine circulation and the krill DVM, which they called an "estuarine pumping system". However, the horizontal distribution of macrozooplankton exhibits a high variability in response to fluctuations in the strength of the aggregation processes. This was evidenced in the St. Lawrence Estuary where dense krill concentrations exhibit an important spatial and temporal variability at meso- and smaller scales (<~100 km or < months) (Simard and Lavoie 1999; Sourisseau et al. 2006). DVM plasticity and asynchronous features (Pearre 2003*a*, 2003*b*) should thus modulate the intensity of the aggregation–dispersion processes and the horizontal organisation. DVM variability at different time scales is well known for several zooplankton species, and among the modulating factors are light (Boden and Kampa 1967; Kaartvedt et al. 1996; Pearre 2003*b*), thermocline, halocline, and oxycline (Sameoto 1980; Spicer et al. 1999), physiological condition (Tarling 2003), food and predator distribution, and individual variability (Price 1989; Onsrud and Kaartvedt 1998; Tarling et al. 2002). Such dynamics should explain the following paradigm for the St. Lawrence Estuary. Coupled physical–biological models, including a two-dimensional (2D) model of the Estuary and laterally averaged current field (Zakardjian et al. 1999) and a 3D model (Sourisseau et al. 2006), concluded that the aggregation of vertically migrating zooplankton in the Estuary can not be generated if the organisms spend more than 6 h in the outflowing surface layers. However, field observations show that euphausiids are present in the surface layer (0–40 m) throughout the night (Simard et al. 1986*b*), and therefore, the two-layer "estuarine pumping system" suggested by Runge and Simard (1990) alone appeared insufficient to explain persistent krill accumulation at the head of the channel (e.g., Simard et al. 2003) if the animals stay in the surface layer overnight.

This krill aggregation constitutes the heart of the baleen whale feeding ground of the Saguenay – St. Lawrence Marine Park (Simard and Lavoie 1999). Krill DVM pattern and variability need to be accurately defined at the fine scale to correctly explain the observed distribution in the St. Lawrence system as a result of the combination of the vertical distribution with the two-layer circulation. The present work is an effort to estimate the detailed fine diel variability of krill vertical distribution. A suite of acoustical and stratified net sampling and pigment-tracing methods is used to examine mass transfer, individual interchanges, and migration speed on the vertical with high resolution. The average DVM pattern is combined with simulated currents at the mouth of the Estuary provided by the 3D regional circulation model (Saucier et al. 2003) to understand the actual dynamic of krill pumping in the Estuary. A great part of the discrepancy between the assumed process of krill aggregation in the Estuary and the simulated results is clarified.

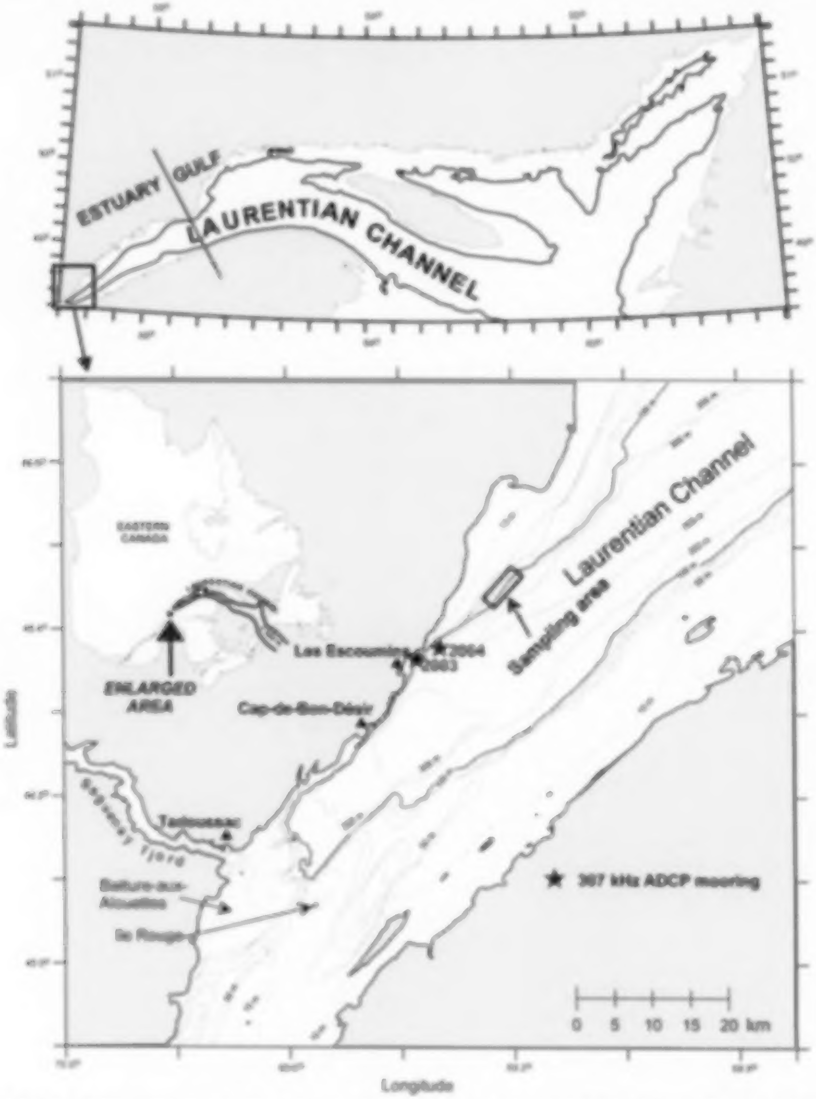
Materials and methods

Intensive sampling was carried out aboard of the R/V *Coriolis II* on 3–7 September 2003 on the north slope of the Laurentian Channel in the St. Lawrence Estuary (Fig. 1), on the entrance path of the regional krill aggregation at the channel head (cf. Lavoie et al. 2000). Zooplankton sampling was done with a 1 m^2 Bioness™ (Open Seas Insrumentation, Inc., Musquodoboit Harbour, Nova Scotia, Canada) with 1 mm mesh size, targeting larger zooplankton species and minimizing possible phytoplankton retention in the collector. The vertical strata were set to four layers representing different hydrodynamic conditions (0–20, 20–40, 40–100, and 100–150 m). Short tows (~15 min) were used to minimize krill stomach pigment degradation and the stress imposed to the organisms. The profiling frequency was slightly above $1 \cdot h^{-1}$, and the zooplankton samples were frozen on board at –80 °C. The zooplankton identification in the laboratory was done as follows: for organisms larger than 10 mm, the whole sample or a fraction with a minimum of 20 euphausiids was analyzed; for smaller zooplankton, mainly consisting of calanoid copepods, the minimum subsample size was fixed to 100 organisms. Four main zooplankton groups were observed (*Meganyctiphanes norvegica*, *Thysanoessa raschi*, *Calanus* sp., and *Themisto libellula*), but only euphausiids, which dominated, are considered in this paper.

Stomach pigment measurements were made on the two euphausiids species *M. norvegica* and *T. raschi*. For each species, a maximum of 20 and a minimum of five living organisms were sorted under artificial light immediately after the net retrieval on board. These organisms were then rapidly frozen at –80 °C to avoid significant degradation of the chlorophyll inside the stomach. The laboratory analyses were then made within 2 months after the cruise. The organisms were thawed (<5 min), and their stomachs were extracted under the microscope, placed in groups of five into 5 mL of acetone (90%), ground up, and left at 4 °C in dark for 14–16 h pigment extraction. Then, the chlorophyll *a* concentrations were estimated with a Turner fluorometer (model TD-700; Turner BioSystems, Sunnyvale, California) following a method without acidification (Welschmeyer 1994). The fluorometer calibration was specific for chlorophyll *a* estimation (Arar and Collins 1997).

Temperature and salinity were measured with a conductivity–temperature–depth meter (CTD; model SBE 19; Sea-Bird Electronics, Inc., Bellevue, Washington) mounted on the Bioness™. In situ fluorescence was measured with a fluorometer (model WS3S; Wetlabs, Philomath, Oregon). Additional profiles were obtained with another

Fig. 1. Location of the sampling area in the St. Lawrence Estuary. The ship followed the 160 m isobath during the sampling. Stars indicate the positions of the acoustic Doppler current profiler (ADCP) moorings. The line on the upper panel shows the cross section of the numerical circulation model separating the Estuary from the Gulf that is used for the krill import simulations.


ESTUARY
GULF
LAURENTIAN CHANNEL
EASTERN CANADA
ENLARGED AREA
Les Escoumins
2004
2003
Cap-de-Bon-Désir
Saguenay fjord
Tadoussac
Batture-aux-Alouettes
Ile Rouge
Laurentian Channel
Sampling area
307 kHz ADCP mooring
0 5 10 15 20 km
Latitude
Longitude

CTD (model SBE 19; Sea-Bird Electronics, Inc.) with oxygen and fluorescence sensors mounted on the rosette. One rosette profile was made after every two Bioness™ tows. Water samples were collected at four depths (5, 10, 20, and 50 m) with Niskin bottles, and 250 mL were filtered on GF/F filters. The filters were then frozen at –80 °C. The laboratory analyses were made within 2 months after the cruise. The chlorophyll *a* was extracted in 10 mL of acetone (90%) and processed as described above for the stomachs.

Acoustics measurements

The hull-mounted 156.3 kHz acoustic Doppler current profiler (ADCP; WH Ocean Surveyor, 30° tilted beam axis; Teledyne RD Instruments, Inc., Poway, California) was used to obtain current velocity and zooplankton backscatter intensity. The vertical resolution was set to 5 m for 60 bins. The first usable bin was centred at a depth of 20.33 m. The five bins immediately above the bottom were eliminated because of bottom echo contamination. Bins from depths of 20 to 125 m were thus available for current and acoustic backscatter analysis. Profiles were collected every 3 s and were averaged over 5 min intervals. The 5 min raw backscatter data were corrected for spreading and absorption losses (Deines 1999) to produce a corrected (but not calibrated) relative volume backscattering strength (S_{vr}).

A second 307 kHz ADCP (WH Sentinel, with 20° tilted beams; Teledyne RD Instruments, Inc.) in a nearby streamlined underwater buoy (ADCP Buoy; Open Seas Instrumentation Inc.) was also moored near the bottom, looking up in the vicinity of the study site (Fig. 1). The ADCP was moored from 3 to 29 September 2003 and from 14 August to 9 October 2004. Average deployment depths were 112 ± 1.2 m and 145 ± 1.6 m, respectively, and distances from the bottom were 13 m and 89 m, respectively. The 65 bins were 2 m high, with the first bin centred at 4.17 m above the ADCP. The six bins directly below the surface were eliminated to remove surface echoes. The S_{vr} estimation was realized as previously, with parameters corresponding to the ADCP model type (from Deines 1999) and sound speeds and absorption coefficients estimated from CTD profiles at the beginning and end of the mooring periods. As in Tarling et al. (2002), a composite image of the S_{vr} over a 24 h period was computed for each month. We used the median as the central statistic instead of mean to minimize the influence of extreme values and asymmetric distributions. For the 3-month series of 2004, additional monthly composite images were computed for the vertical velocity, corrected for a ~ –4 mm·s^{-1} global bias, obtained by integrating over all depths and time series and median-filtered with a 6 m × 50 min kernel to filter out high-frequency variability. Such a 24 h low-pass filtered estimate of ADCP vertical velocity is interpreted as a proxy for vertical swimming speed (e.g., Tarling et al. 2002; Jiang et al. 2007). As in Jiang et al. (2007), we then imposed a condition to consider the vertical velocity estimate of each bin as valid. This condition required that a minimum of 25% of good pings were used when the ADCP firmware computed the three- or four-beam Doppler solution for the bin. Also, to compute the monthly composite, bins in which nonvalid velocity occurred more than 50% of the time were excluded. As in Jiang et al. (2007), the median S_{vr} in the 10–30 m stratum was computed for the 2004 series to trace the timings of the krill scattering layer (SL) arrival and departure from the upper water column along the 3-month period. Similarly, the ascent and descent timings were traced from the time series of the median vertical velocity of the 60–70 m midwater-column stratum.

The acoustic system used for biomass estimations was a Simrad EK60 scientific echosounder (Kongsberg Maritime AS, Horton, Norway), with two hull-mounted split-beam transducers operating at 120 kHz (3°) and 38 kHz (7°). The ping repetition rate was 1·s^{-1}, which corresponds to a horizontal distance of 1.29 m at a Bioness™ sampling speed of 2.5 knots. The upper 12 m (range 7 m) of the water column were ignored because of necessary initial blanking and contamination by ringing. The acoustic system was calibrated with the standard sphere method for each frequency (Foote et al. 1987). The Simrad EK60 raw data were converted to HAC standard format via ER60 and analysed with the CH2 echo-integration and editing software (Simard et al. 2000). Volume backscattering data exceeding the estimated noise level profiles were kept for echo-integration at 38 and 120 kHz. Three echo-integrations were performed (volume backscattering index metric, s_v, in m^2·m^{-3}; Simmonds and MacLennan 2005). The first one was done with the 120 kHz data using 2 m vertical × 10 s (10 pings) bins for a comparison with Bioness™ zooplankton samples. The second and third echo-integrations were made with the 120 and 38 kHz data using a resolution similar to the onboard ADCP S_{vr} bins (5 m × 5 min). Contaminations from ADCP transmissions, whales swimming through the acoustic beam, and occasional wrong pings due to bubble clouds near the transducer were excluded from the data. Copepods did not significantly contribute to the backscatter strength because of their relatively low densities (maximum 50 individuals·m^{-3} during the first 52 h) and low mean target strength $\mathrm{TS_N}$(~ –103 dB for a 2–3 mm copepod at 120 kHz (Stanton and Chu 2000; Mair et al. 2005)), which would give volume backscattering strengths ($S_{v,120}$ = 10log(s_v) = $\mathrm{TS_N}$ + 10log(individuals·m^{-3})) smaller than –86 dB re 1·m^{-1}. Similarly, the contribution of the hyperiid amphipod *T. libellula* to the S_v was negligible because of their very low mean densities (0.13 individuals·m^{-3}) relative to euphausiids.

Conversion of S_v to biomass was identical to that presented by Simard and Lavoie (1999) and Cotté and Simard (2005). From the size distribution of the krill sampled, a conversion factor $\overline{\mathrm{TS}}_w$ of –69.13 dB·g^{-1} was computed, which is identical to the value of –69 dB·g^{-1} computed for other surveys in this area by these authors owing to the stability of the krill size distribution. A conversion factor of –69 dB·g^{-1} was thus applied for our conversion to get biomass per cubic metre (B):

$$B = s_v/10^{(\overline{\mathrm{TS}}_w/10)}$$

Results

Physical conditions

A thermocline oscillating around 10–20 m separated the surface (0–20 m) and subsurface (20–40 m) waters (salinities, 29–30 and 30–31.5 PSU, respectively; temperatures, >4 and 1.5–4 °C, respectively) (Fig. 2). Underneath, a cold (–0.5 to 1.5 °C) intermediate layer (CIL), between 40 and 100 m depths, overlaid the Atlantic waters with salinities >33 PSU and temperatures >1.5 °C, which were more prominent around high water. Horizontal velocities from the onboard ADCP were strongly tidally modulated, with strongly barotropic along-channel flood currents towards the head of the channel and the inverse during ebb, albeit less barotropic with increased shears near the pycnocline, the reversals lagging the tidal amplitude by about 1–3 h (Fig. 3*a*). Cross-channel currents were much weaker and more baroclinic, characterized by northward flow in upper water column around high water (Fig. 3*b*). Tidal streams were evident in the upper layers (<40 m), with north coast headings for a few hours after low water and the inverse thereafter. Below 50 m, the currents were more variable and the tidal imprint was less apparent.

Krill distribution

DVM of *M. norvegica* and *T. raschi* were evident from the stratified Bioness™ samples (Fig. 4). During daytime, all krill was below 40 m, within the CIL and the deep layer. During the first two nights (4 to 6 September), between 1900 and 0500, 60% to 80% of the euphausiid population was above 40 m, which leaves a significant part of the population below 40 m. On 5–6 September, for 3 h around midnight, the *M. norvegica* population largely left the surface layer (0–20 m; Fig. 4*a*). On the last night, the relative zooplankton (krill and copepods) concentration in the upper layers was higher. This apparent change in vertical distribution was as-

Fig. 2. (*a*) Tide level from the Canadian tide and currents tables and (*b*) density, (*c*) temperature, and (*d*) salinity measured by the Bioness™ during the sampling. Bold lines in (*c*) and (*d*) separate the four layers. Hatched area corresponds to missing data, and white dotted lines correspond to Bioness™ profiles. Note: through the paper, time is expressed using the 24-hour system; in the figures, however, the numbers have been truncated for readability, for example, 1200 is expressed simply as 12.

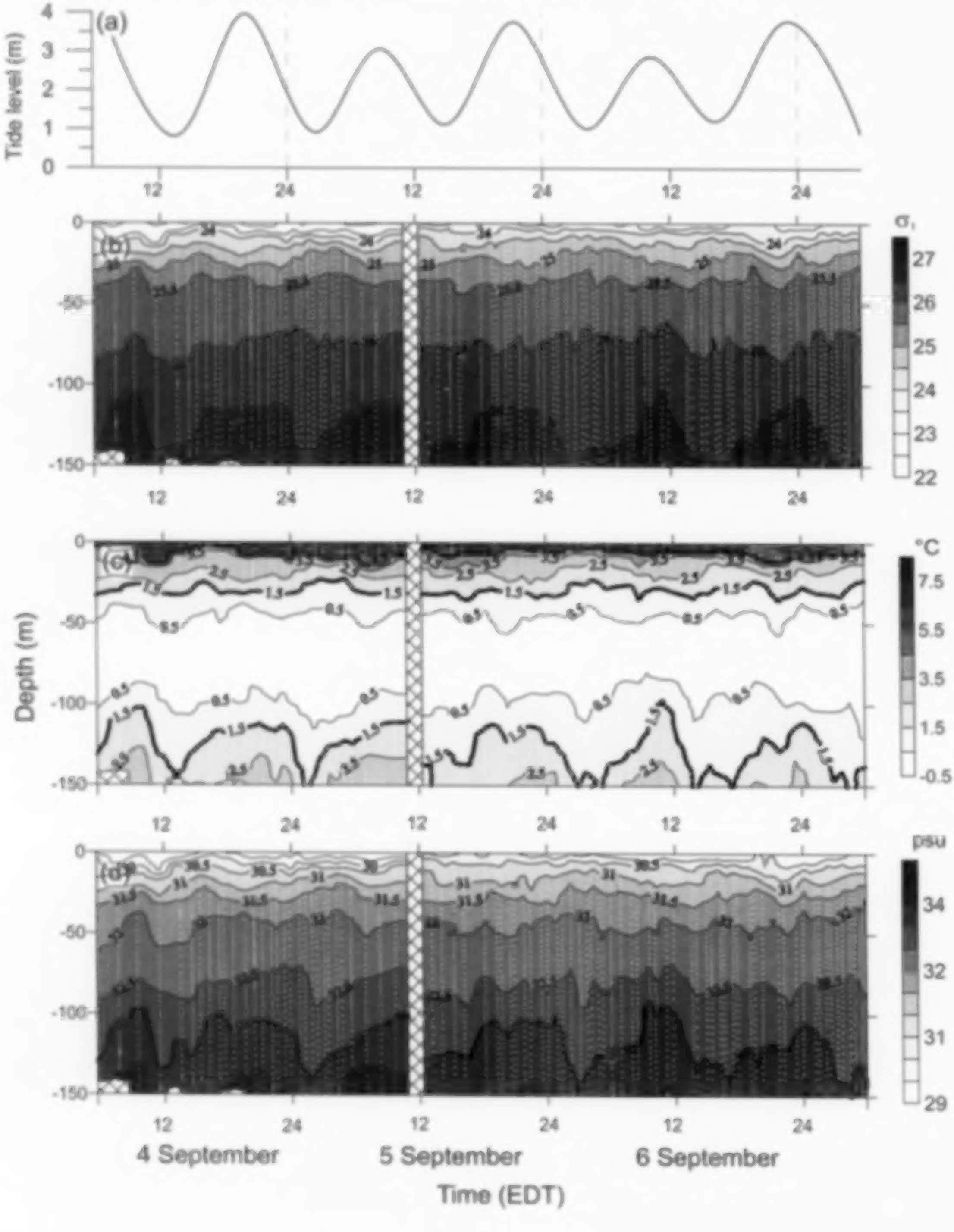
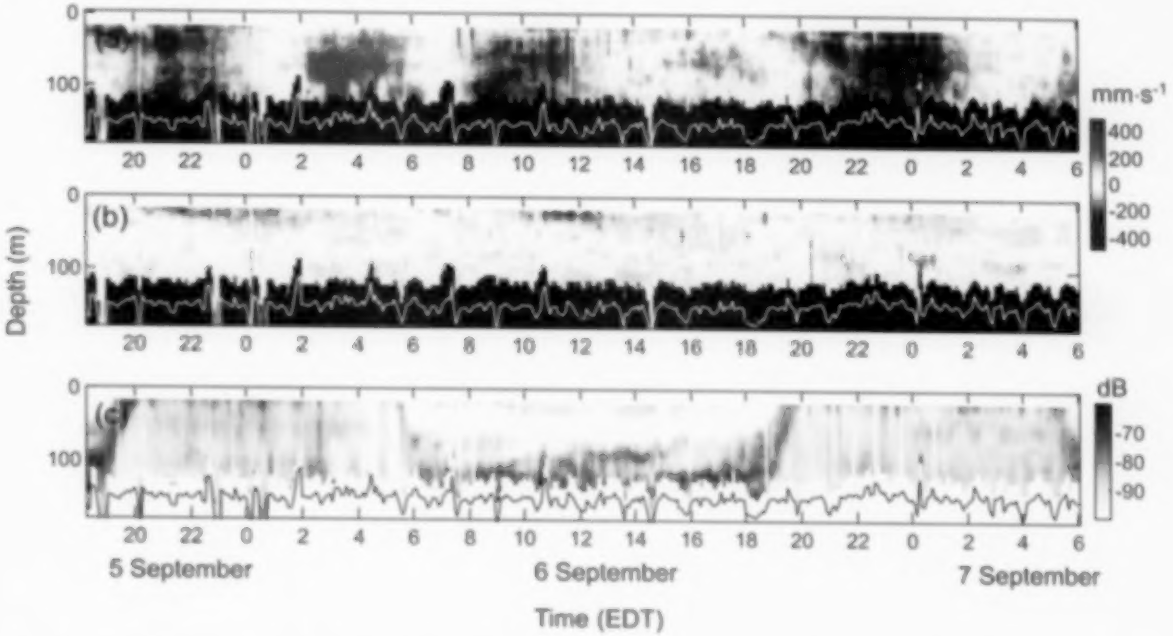


Fig. 3. Measurements from the onboard 153 kHz acoustic Doppler current profiler (ADCP) from 5 (at 1817) to 7 (at 0602) September 2003. (*a*) Along-channel and (*b*) cross-channel current velocities. Negative values are oriented toward the head of the channel and to the north shore. (*c*) Uncalibrated relative volume backscattering strength (S_{vr} rel dB). See Fig. 2 caption for note regarding expression of time.



sociated with an increase by a factor 5 of the zooplankton abundance inferred from the Bioness™ and integrated over the entire water column. From 2100 on 3 September to the end of the sampling period, the maximal concentrations of *M. norvegica* and *T. raschi* inferred from the Bioness™ in the surface layer changed, respectively, from 5 and 20 individuals·m^{-3} to 50 and 80 individuals·m^{-3}.

Acoustic data

The S_v at 120 kHz was mainly due to euphausiids (Figs. 4 and 5*b*). The log–log regressions of the acoustic estimates of krill biomass against Bioness™ catches were significant ($r^2 > 0.24$, $p < 0.05$) for both daytime and nighttime, with slopes of 1.88 and 0.85, respectively. The highest krill concentration estimated from the $S_{v,120}$ occurred during daytime, between 100 and 150 m, whereas the net catches were highest during the night. The $S_{v,120}$ reached –60 dB re 1 m^{-1}, which corresponds to 50 euphausiids·m^{-3} or 14 g·m^{-3}. A weak SL ($S_{v,38}$ = –80 dB; Fig. 5*a*) in the surface layers in daytime (between 0700 and 1800) was classed as small fish by the S_v difference between the two frequencies ($S_{v,120-38}$ near 2 dB; Fig. 5*c* for significant backscatter, where $S_{v,120} >$ –90 dB and $S_{v,38} >$ –95 dB). Several single fish tracks were clearly visible on the echogram when the ship was not moving. These tracks were good candidates to measure the in situ $\mathrm{TS}_{N,120}$ of these fishes from the split beam analyses, which revealed to be ~ –60 dB. During nighttime, small individual targets with $\mathrm{TS}_{N,120}$ between –50 and –70 dB emerged from the bottom. They were likely fish (probably small demersal fish and capelin) and northern shrimp (*Pandalus borealis*) that were caught by the Bioness™ (one to five organisms per sample) in the bottom layer and corresponded to a $S_{v,120} - S_{v,38}$ difference of ~2 dB (Fig. 5*c*).

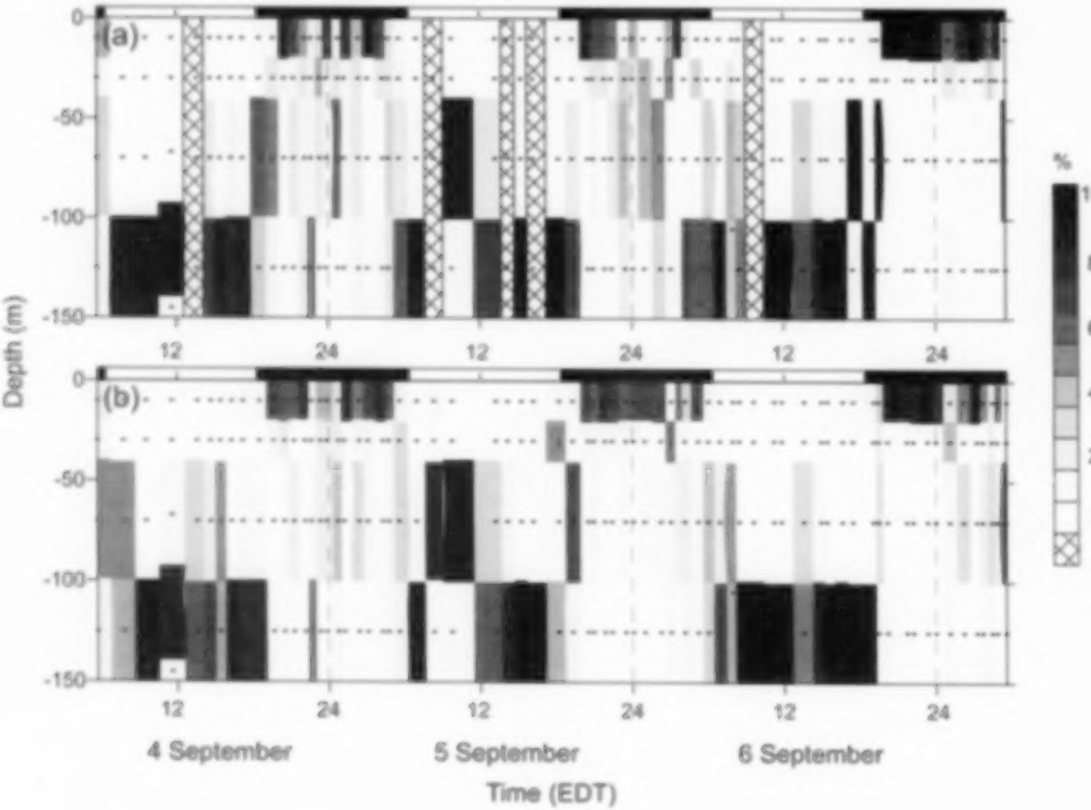
The ascent of the krill SL to the surface layers started at 1800, which corresponded to sunset, and the organisms reached the surface in 1 h. The descent at dawn was well defined on 7 September and took place between 0500 and 0600 (Fig. 3*c*), which corresponded to sunrise. On 6 September, however, the descent was less sharp, which was also noted on the ADCP S_{vr} and stratified net samples (Figs. 4*a*–4*b*). A substantial part of the euphausiid population had migrated downwards well before sunrise. Soon after the ascent, a weak SL reappeared between 100 and 130 m, and significant S_v was present at intermediate depths during the night (Fig. 5*b*).

Chlorophyll distribution and krill stomach content

The chlorophyll *a* concentration from the Bioness™ in situ fluorometer showed high values in the upper 20 m (2–15 mg·m^{-3}) (Fig. 6*a*). The concentration was highest at the surface and rapidly decreased to near 0 at 25–30 m. Chlorophyll *a* extracted from water samples gave the same general pattern (Fig. 6*b*). The average chlorophyll *a* concentration in the surface layer steadily increased over the three days. The highest concentrations (>12 mg·m^{-3}) were observed on the last day at the same time that the zooplankton concentration increased.

The average chlorophyll *a* stomach contents of *M. norvegica* and *T. raschi* over all layers increased during the night (Figs. 6*c*–6*d*). One hour after the ascent, the chlorophyll *a* concentration in the krill stomachs sampled below 100 m was as high as for those sampled in the surface layers. In

Fig. 4. (*a*) *Meganyctiphanes norvegica* and (*b*) *Thysanoessa raschii* vertical distribution (%) observed from 4 to 7 September 2003 by the net sampling. Dashes represent Bioness™ samples and hatched areas correspond to the lack of organisms over all the vertical profile. Day and night are indicated above each plot by open and solid horizontal bars, respectively. See Fig. 2 caption for note regarding expression of time.

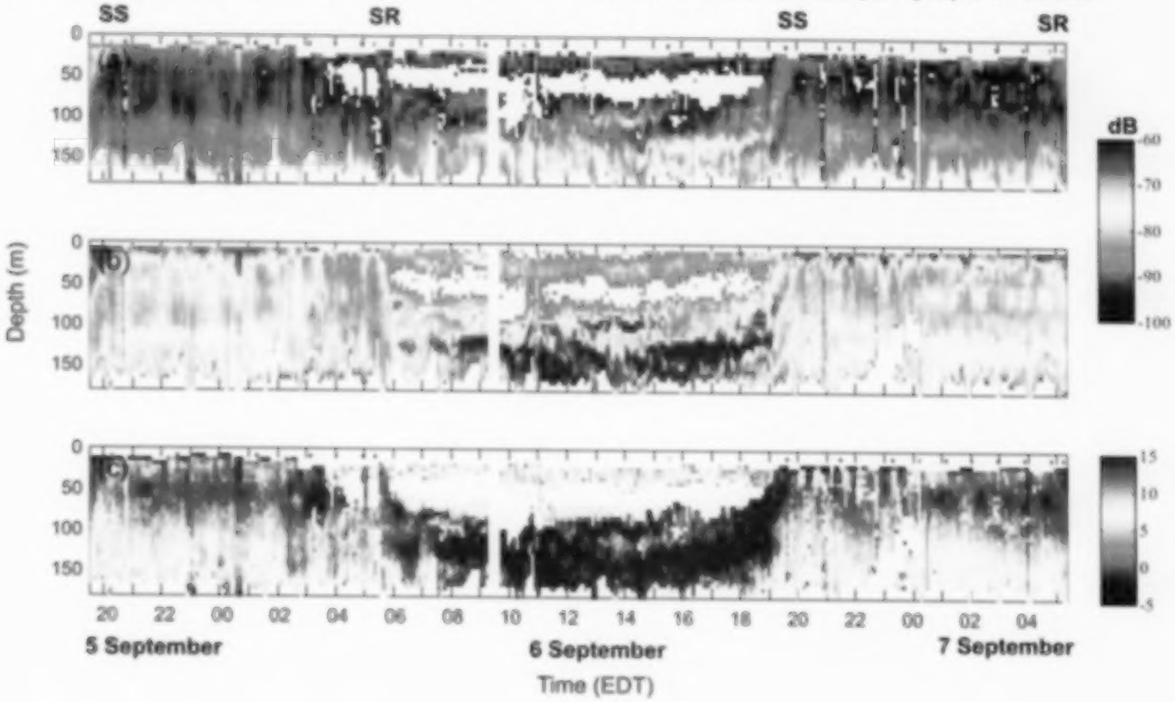


daytime, the chlorophyll *a* in the stomachs decreased exponentially with time. For *M. norvegica*, the fluorescence signal reached its background value at 1200 (around 10 ng·individual^{-1}), several hours after the dawn descent. For *T. raschi*, the background signal was lower than the measurable concentration, and the daytime concentrations were arbitrarily set to zero. A trend to higher average chlorophyll *a* content was observed over the three days for both species and was associated with the increase of the average chlorophyll concentration in surface waters. The maximum chlorophyll *a* stomach concentration increased by one order of magnitude between the first and third day, changing from 100 to >1000 ng·individual^{-1} for *M. norvegica* and from 7 to >65 ng·individual^{-1} for *T. raschi*. *Meganyctiphanes norvegica* stomach pigment content tended to increase during night. For example, the chlorophyll *a* concentration in stomach changed from 10 to 100 ng·individual^{-1} from 2000 to 0600 during the first night.

Acoustic data from moored ADCP

The high-resolution stratified Bioness™ samples confirmed that krill was the main component of the high-frequency sound backscattering observed by the vessel-mounted ADCP and EK60 echosounder. During September 2003, the ascent and descent clearly showed up at ~1900 and 0530 on the composite 24 h S_{v} echogram of the moored ADCP (Fig. 7*a*) in accordance with sunset and sunrise and vessel survey (Figs. 3*c* and 5*b*). The series of similar echograms for August to October 2004 clearly evidenced the photoperiod effect on the DVM (Figs. 7*b*, 7*d*, and 7*f*). From August to October, the ascent advanced from 2000 to 1800 and the descent was delayed from 0530 to 0630. This lengthening of DVM nocturnal phase almost perfectly matched the lengthening of the night (Fig. 8*a*). The arrival in the surface layer was ~30–60 min after sunset and departure was ~15–0 min before sunrise. As with ship-based S_{v}, the S_{v} below 80 m on all monthly composite echograms was minimal during the 2 h window following the dusk ascent in which all the krill SL took part (Figs. 7*a*, 7*b*, 7*d*, 7*f*). Soon after the ascent, some krill started to redistribute over the whole water column and the deep SL started to reform, giving rise to a bimodal nocturnal vertical distribution. During some nights, clear descent trajectories were evident on the S_{v} high-resolution time series (not shown). S_{v} at intermediate depths was often significant, especially around midnight (e.g., Fig. 7*b*). The dense SL in surface layers also tended to

Fig. 5. Volume backscattering strength (S_v, dB re 1 m^{-1}) from 5 to 7 September 2003 at (*a*) 38 and (*b*) 120 kHz from the Simrad EK60 echosounder. Vertical and horizontal resolutions are 2 m and 5 min, respectively. (*c*) The S_v difference at the two frequencies ($S_{v,120} - S_{v,38}$) was calculated to classify the echoes except for blanked areas with insignificant backscatter and low signal to noise ratios ($S_{v,38} < -95$ dB and $S_{v,120} < -90$ dB). SS, sunset; SR, sunrise. See Fig. 2 caption for note regarding expression of time.



thicken around midnight but concentrated again in a thinner layer before dawn. The composite S_{vr} echograms show that the deeper daytime depth was reached a couple of hours after the bulk descent. A mirror pattern is shown before the ascent. However, the high-resolution S_{vr} series showed a substantial amount of small-scale variability around this general trend for both day and night patterns over the water column, likely partly in response to krill small- and mesoscale patchiness and advection. The monthly composites of low-pass filtered vertical velocity (Figs. 7*c*, 7*e*, 7*g*) evidenced the bulk ascent and descent at sunset and sunrise and the substantial nocturnal descent starting just after the ascent and extending until about midnight. The ADCP data indicated a trend to increased swimming speed along the ascent (e.g., Fig. 7*c*).

A weaker vertically migrating SL was observed in the surface layer during daytime on the ADCP time series (Figs. 7*a*, 7*b*, 7*d*, 7*f*). Examination of the S_{vr} on the four beams of the ADCP separately indicated that this SL was not homogeneous, which is indicative of more patchy distributions of scatterers, likely fish aggregates (Jiang et al. 2007). This SL was similar to the fish SL (likely capelins according to Bioness™ catches) observed by the ship echosounder in the surface layer during the day (Figs. 5*b*, 5*c*). These organisms had another light intensity preferendum. Like krill, they avoided the surface layer during daytime but formed a loose SL around 30 m depth.

Discussion

Despite a little contamination by other sparse species, possible masking effects of 3D krill patchiness and shearing advection, the acoustic data from both the ADCPs and the EK60 echosounder clearly showed strong krill DVM with fine resolution details. Stratified sampling with the Bioness™ corroborated the SL composition, with a $S_{v,120} - S_{v,38}$ signature of 10 to 2 dB, typical of local krill during daytime (Simard and Lavoie 1999). Both direct sampling and acoustic data sets exhibited significant variability resulting in low global correlation between the acoustic and direct sampling, likely largely due to 3D misalignment of both types of samples, their differing sampling volumes, krill patchiness, and the relative diel catchability and bias of the two gears as revealed by the differing $S_{v,120}$ versus krill catch slopes during daytime and nighttime (Miyashita et al. 1996; Wiebe et al. 2004; Chu and Wiebe 2005). Examining this sampling gear performance is out of the scope of this paper and will be discussed elsewhere.

DVM dynamic pattern

The average krill DVM pattern during our sampling period appears to be as follows. In daytime, krill was concentrated in a dense SL below ~90 m. A few hours before sunset, individuals near the upper boundary of the SL slowly began to migrate upwards. This motion accelerated at sunset, when essentially all the SL joined these early migrants,

Fig. 6. Chlorophyll *a* (Chl *a*) vertical distribution ($mg \cdot m^{-3}$) estimated by (*a*) the Bioness™ in situ fluorometer and (*b*) water samples from 4 to 7 September 2003. Chl *a* stomach contents (ng Chl $a \cdot individual^{-1}$) for (*c*) *Meganyctiphanes norvegica* and (*d*) *Thysanoessa raschi*. Dots (*a*), arrowheads (*b*), and dashes (*c* and *d*) indicate samples and Bioness™ profiles, and hatched areas correspond to (*a*) missing values or (*c* and *d*) a lack of organisms. See Fig. 2 caption for note regarding expression of time.

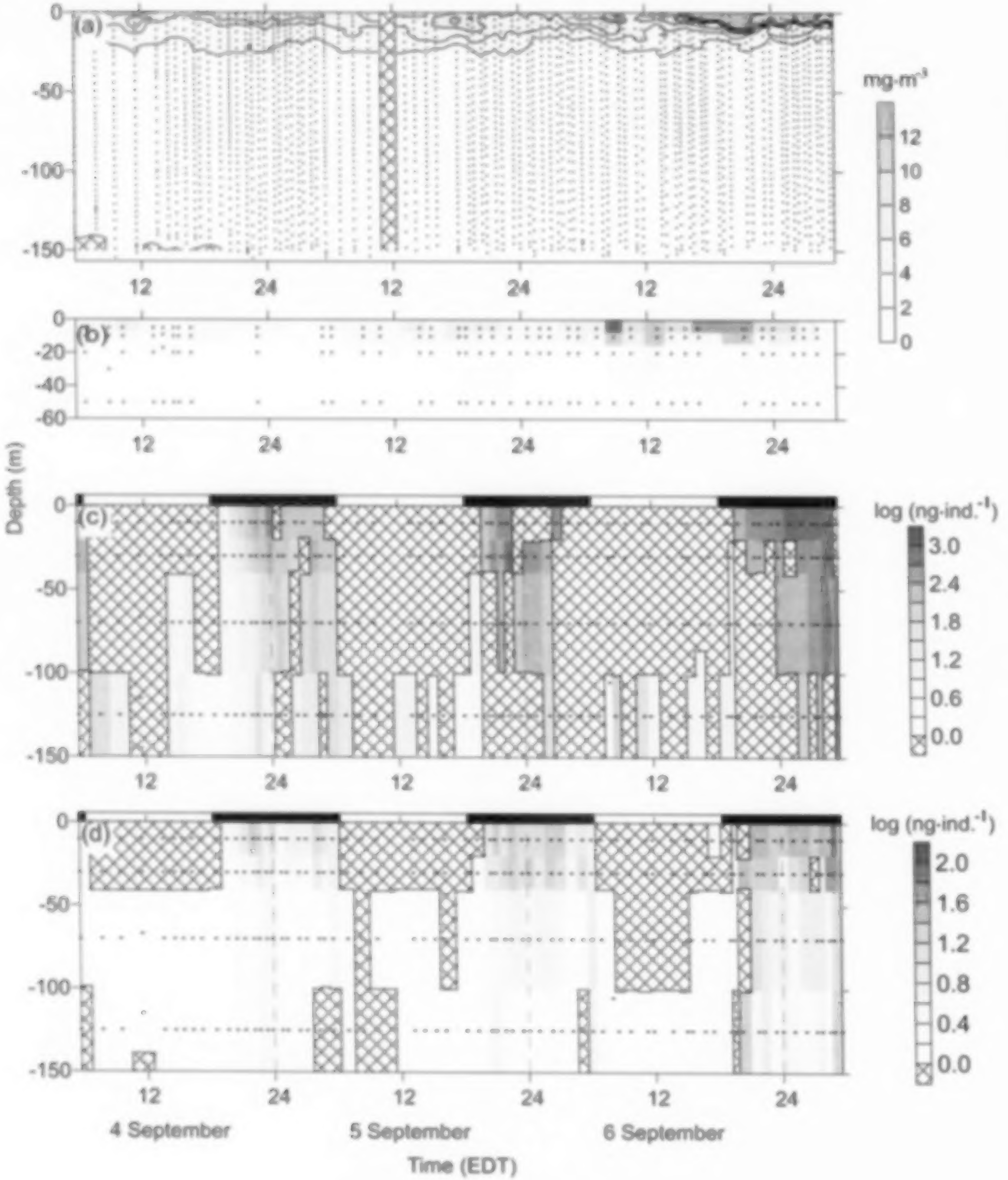
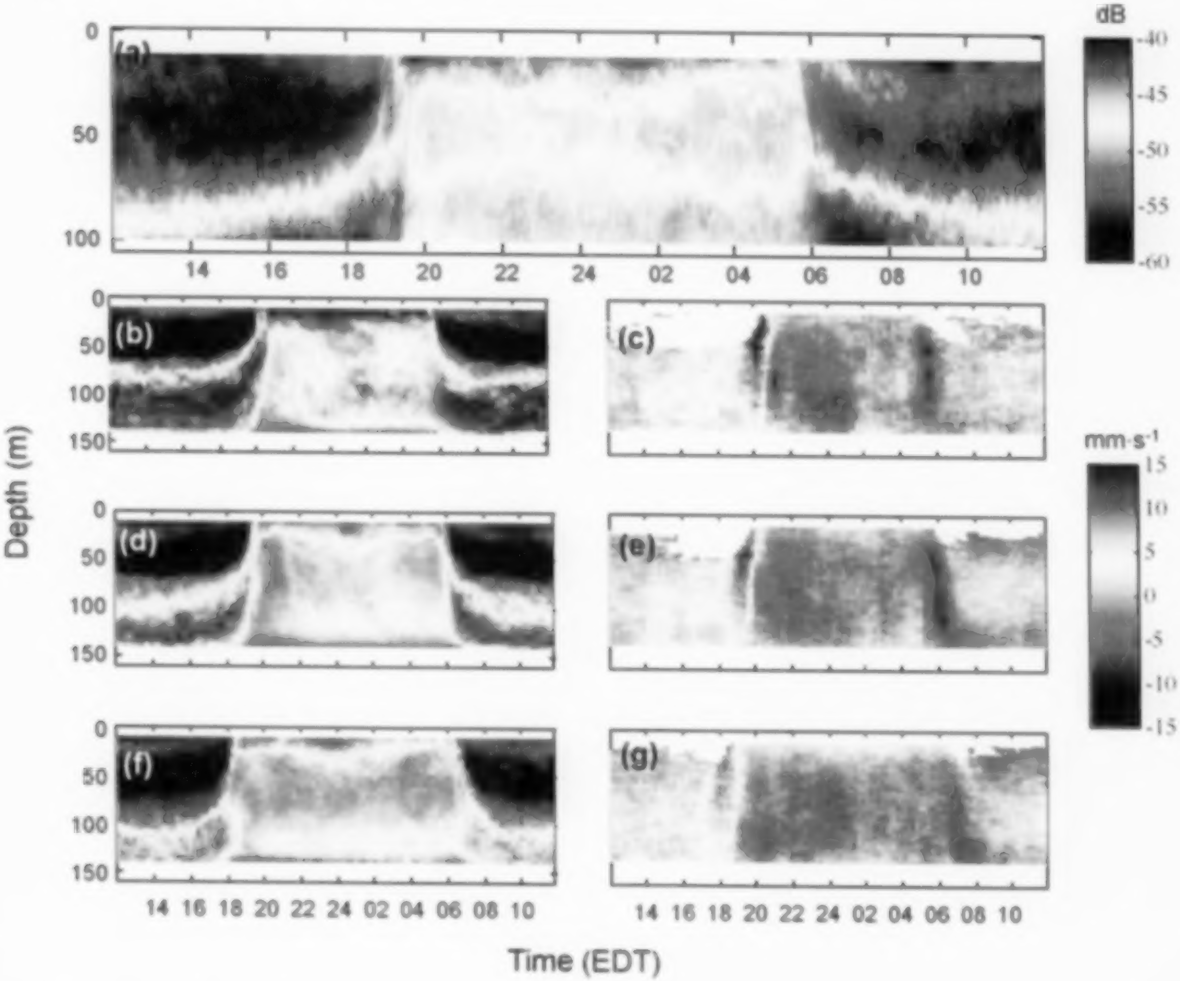
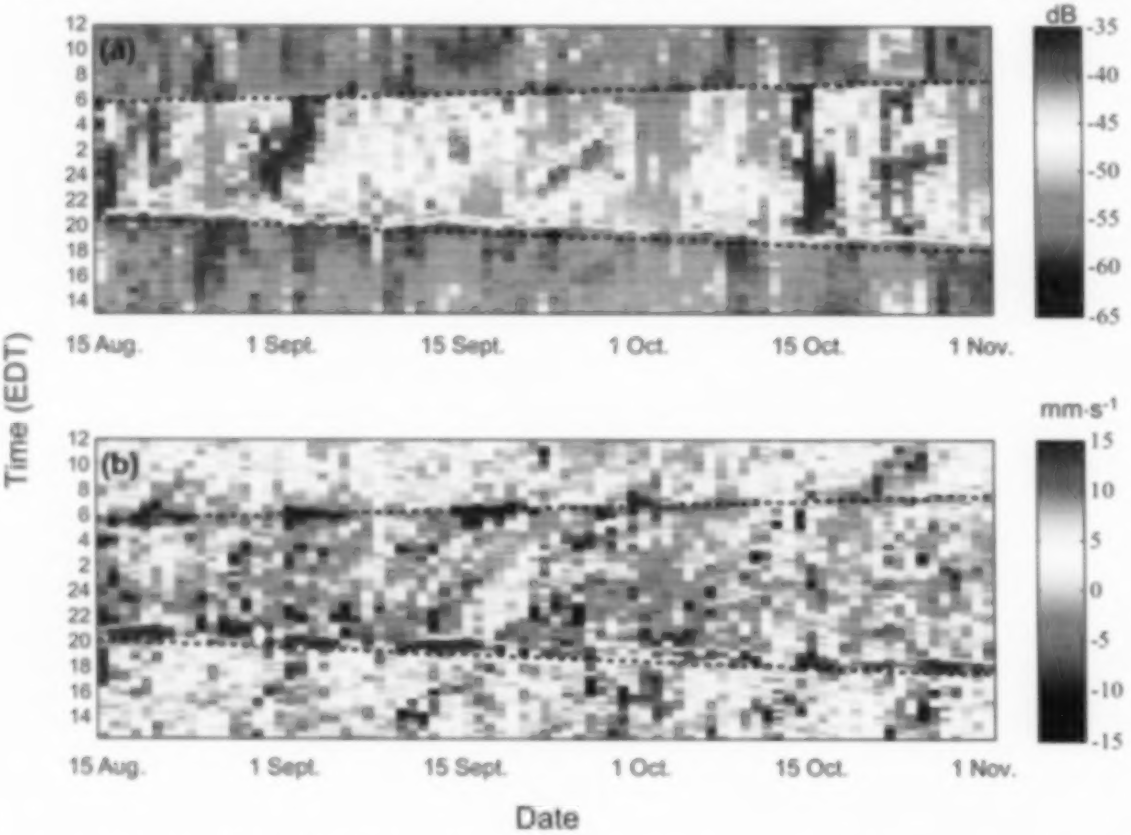


Fig. 7. Twenty-four hour composite images of uncalibrated relative volume backscattering strength median (S_v, rel dB) from the 307 kHz moored acoustic Doppler current profiler (ADCP) series in (*a*) September 2003, (*b*) August, (*d*) September, and (*f*) October 2004, with (*c*, *e*, *g*) corresponding low-pass filtered vertical velocity median for 2004. Blank areas correspond to nonvalid velocities. See Fig. 2 caption for note regarding expression of time.



reaching the surface layer in about 1 h at an average vertical swimming speed of ~150 m·h^{-1} (42 mm·s^{-1}) in agreement with results from other studies (Hardy and Bainbridge 1954; Tarling et al. 1999; Thomasson et al. 2003). Estimates of median vertical speed of the ascent from the ADCP monthly composites were about 50% lower. This bias (also noted by Heywood (1996) and Tarling et al. (2002)) is likely due to the necessary time–depth smoothing window used in processing the noisy high-resolution ADCP vertical velocities, themselves obtained by averaging over all individuals insonified in the time–depth sample bins. The observed increase in vertical swimming speed at the end of the ascent may indicate a sorting of the krill by swimming speeds in the final step when the barrier isolume controlling the ascent is no longer acting and the rate of change in light intensity is peaking (cf. Tarling et al. 2002). As soon as 1 h later, the newly formed surface SL starts to disperse over the water column and reform a deep SL between 90 and 130 m. The ADCP velocity then indicates downward swimming krill over all subsurface layers, starting immediately after the SL reached the surface and extending to midnight. This downward movement appears as active swimming and not passive sinking. This is supported by the fact that the downward velocity is as fast as that of the descent, the occasional observations of synchronous nocturnal descents with slopes mirroring the ascent on the DVM pattern of the high-resolution S_v time series, the rapid formation of the SL at depth, and the stomach pigment content of its krill. The increase of stomach pigments over the night at each depth for both species tends to confirm the continuing downward movement observed by ADCP vertical velocities during a large part of the night, despite the complex dynamics of the

Fig. 8. (*a*) Time series of 24 h periods with a 10 min resolution of the uncalibrated relative volume backscattering strength (S_v, rel dB) median over the 10–30 m layer from the 307 kHz moored acoustic Doppler current profiler (ADCP) in 2004, and (*b*) similar two-dimensional time series for the low-pass filtered vertical velocity median in the 60–70 m layer, showing the bulk ascent and descent times. The superimposed broken lines indicate sunset and sunrise time series. See Fig. 2 caption for note regarding expression of time.



in situ stomach pigments (Moloney and Gibbons 1996). Although the bimodal vertical distribution is maintained overnight on average, day-to-day variability is observed. A change in krill vertical dynamics appears to occur around midnight, as indicated by the trend to higher S_v at intermediate depths, the end of the thickening of the dense surface SL, and the vanishing of the downward swimming speed over the water column. Is this an indication that part of the krill is initiating a second intensive feeding bout before dawn? The absence of increasing S_v in the deep SL when downward swimming ended and nonrenewal of the stomach pigments of its main constituent for *T. raschi* all tend to support this hypothesis of a predawn meal (cf. Simard et al. 1985). This is less evident for the less abundant *M. norvegica*, though its catches and stomach pigment content on 4 and 5 September are in favour of such a possibility. The final descent is initiated by the first gleam of light some 15 min before sunrise, with a swimming speed similar to that of the ascent. The density of the descending SL is lower than that of the ascending one at dusk because a significant fraction of the krill has already returned to their daytime depth. After the bulk descent, the daytime depth tends to continue to deepen until noon before the cycle is resumed. In summary, the average DVM pattern includes two synchronous twilight vertical movements, synchronised by changing light intensity, and asynchronous nocturnal migrations, marked by a change of dynamics at midnight likely from a change of vertical migration direction from part of the krill. Stomach content tracing and the general pattern are all supportive of the DVM hunger-satiation hypothesis (Pearre 2003*a*). The observed higher proportion of krill catches in the surface layer during the third night when the phytoplankton concentration was higher is not incoherent with this model, as the nocturnal vertical pattern of stomach pigments was maintained, and the formation of nocturnal deep and intermediate SLs repeated on the ship's echogram. The apparent inconsistency from net samples may result from masking due to krill patchiness and differential advection history in the vertical, which can not be ruled out from the 3D current structure.

All krill synchronously migrate to the surface at dusk to feed; satiated individuals rapidly swim back to their daytime depth and reform a deep SL while others continue to feed in surface waters. Around midnight, a larger part of the population is satiated and leaves the surface layer. Some krill rejoin the deep SL but others go back to surface to feed again before the increasing light intensity at dawn brings them back to their daytime depth. Natural variability in krill and phytoplankton patchiness, diet (Kaartvedt et al. 2002), feeding history, and physiological state, combined with tidal and other frequency fluctuations in 3D circulation patterns, produce a variety of realisations of this general model. As pointed out by Pearre (1979, 2003*a*, 2003*b*), the sampling requirements to evidence this complex vertical behaviour are seldom met. Adequate DVM tracking for a single species is difficult; simultaneously tracking several members of the community at different trophic levels is much more complex (cf. Tarling et al. 2002; Pearre 2003*b*), and requirements in gears diversity and simultaneous sampling platforms are beyond the means of usual research. High-resolution acoustics (ADCP, multifrequency, and others) has improved our means of tracking mass movements on the vertical and, to a certain degree, the bulk vertical swimming speed of scatterers, but tracking interchanges and validating acoustics with direct sampling are still difficult and time-consuming, and controlling for masking effects of 3D patchiness and advection requires special attention.

The ADCP time series during fall provided evidence of photoperiod control on DVM timing. Further studies should extend such observations to the winter period to monitor the effect of the change of in situ light intensity by the presence of the sea ice cover, generally present between January and April in the Gulf and Estuary. As observed in arctic environments (Blachowiak-Samolyk et al. 2006; Cottier et al. 2006), the krill should adapt their behaviour to maximize their fitness, and the asynchronous component of the vertical migration within the population may become more important.

Implication on mesoscale krill advection

The effect of nocturnal asynchronous migrations and vertical distribution on krill advection into the Estuary from the Gulf was assessed by estimating the transport on the 44 km long cross section at the mouth of the Estuary by coupling the average DVM pattern with simulated currents from the 3D regional circulation model (for details, see Sourisseau et al. 2006). Three-year (1997 to 1999) simulated currents were averaged. Cross-sectional mean currents above 40 m are downstream at 150 $m \cdot h^{-1}$ and upstream in the CIL (40–100 m) and below (100–150 m) at 52 and 32 $m \cdot h^{-1}$, respectively. Assuming no nocturnal spreading of the krill over the water column and a diel residence time of 10 ± 2 h above 40 m and 14 ± 2 h below 100 m, krill would be flushed out of the Estuary at an average speed of about 43.8 $m \cdot h^{-1}$. This is in agreement with regional modeling studies of DVM-trained zooplankton (Zakardjian et al. 1999; Sourisseau et al. 2006) indicating that the average ratio of time spent in the deep layers (100–150 m) relative to surface layers (0–40 m) must be higher than five (20/4) to maintain zooplankton in the Estuary.

Assuming that 30% of the population is spread over the water column during the night, starting 2 h after the ascent, the average time spent in September in the surface layers, the CIL, and the deep layer are now 7, 3, and 14 $h \cdot day^{-1}$, respectively. Even with such DVM behaviour, the individuals are flushed out of the Estuary by the laterally averaged currents at the cross section at mouth of the Estuary, but at a slower speed (18.2 $m \cdot h^{-1}$). The exact fraction of the population below 40 m during the night was not accurately evaluated acoustically because acoustic information in the first metres (0–12 m) was lacking and the average krill tilt-angle profile during night was unknown. The 30% gross estimate comes from the Bioness™ samples, which also contain a level of uncertainty due to diel change in krill catchability as evidenced by the day–night S_v vs. catch regressions.

Previous results from a 3D modeling study (Sourisseau et al. 2006) concluded that krill import on the cross section must occur mainly on the north side of the Estuary. Cross-sectional mean current profiles were computed for the first 15 km segment from the north shore. The currents in the 0–40 m layer are then downstream at a speed of 97 $m \cdot h^{-1}$ and upstream at –77 and –49 $m \cdot h^{-1}$ in the 40–100 and 100–150 m layers, respectively. The krill advection using the above average DVM model is now upstream at an average speed of 10 $m \cdot h^{-1}$. These new estimates show that the observed average DVM model incorporating nocturnal vertical spreading of a fraction of the krill is insufficient to explain the observed persistent retention of the krill in the Estuary and the resulting dense mesoscale aggregation at the head of the deep Laurentian Channel in the Saguenay – St. Lawrence Marine Park (Simard and Lavoie 1999). The 3D current structure in the Estuary must be an essential component for advecting and importing krill into the Estuary from the sourcing Gulf.

The following processes appear necessary to explain the krill recruitment and aggregation at the head of the Laurentian Channel in the St. Lawrence Estuary. In agreement with Runge and Simard (1990), the first one is the flow of the CIL and the deep layer towards the head of the channel, but as expected by Simard et al. (1986*a*), the cyclonic structure of circulation within the Estuary, with an inflowing current along the north shore and an outflowing coastal jet flushing the Estuary on the south shore, is an intrinsic part of the process that must be carefully taken into account. Cross-channel-averaged currents or coarse grid modeling can not reproduce the actual krill aggregation, as Sourisseau et al. (2006) clearly demonstrated recently, and the krill import may occur mainly in a thin filament along the northern slope of the Laurentian Channel. This process is enhanced by the presence of wind-driven upwelling and Ekman transport on the north side, reinforcing the slope concentrating process (e.g., Cotté and Simard 2005). The second controlling component is the krill DVM pattern, the persistent nocturnal spreading of a substantial fraction of the population over the inflowing CIL, and the DVM seasonal structure. The above findings emphasize the importance of monitoring the circulation at the mouth of the Estuary and wind-generated upwelling on the north shore in an effort to provide good proxies for predicting krill biomass supply to the Estuary and the Marine Park aggregation. They also point out the need to improve our knowledge of the seasonal component of krill DVM behaviour, particularly for the period of sea ice cover. This information should help us to understand the ecological system upon which mammal populations exploiting this resource rely. It should also contribute to base management and protection decisions on sound scientific knowledge, in particular for the Saguenay – St. Lawrence Marine Park at the head of the lower St. Lawrence Estuary and the adjacent areas that are being considered for the establishment of a marine protected area.

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Spatial variation in fishing intensity and its effect on yield

Stephen Ralston and Michael R. O'Farrell

Abstract: Fishing mortality is rarely, if ever, evenly distributed over space, yet this is a common assumption of many fisheries models. To evaluate the effect of spatial heterogeneity in fishing mortality on yield, we constructed age-structured models that allowed for differing levels of fishing in three regions within the boundaries of a stock and explored alternative assumptions about the life stage in which density-dependent compensation operates. If the fishing mortality rate (F) is not excessive (*i.e.*, $F \leq F_{\mathrm{MSY}}$ defined for the spatially homogeneous case; MSY, maximum sustainable yield), simulations demonstrated that minor to moderate spatial variation in fishing intensity does not impact sustainable yield. However, if fishing mortality is excessive ($F > F_{\mathrm{MSY}}$), spatial variation in fishing intensity often improves yield and can actually produce yields in excess of MSY when compensation occurs after dispersal, and the density-dependent recruitment rate is a function of the local density of adults. The yield premium generated in these simulations by postdispersal density dependence is due to a low level of compensatory mortality in heavily fished areas coupled with dispersal of propagules into these areas from lightly fished adjacent regions.

Résumé : La mortalité due à la pêche est rarement, et probablement jamais, répartie de façon uniforme dans l'espace, bien qu'on le présuppose couramment dans plusieurs modèles des pêches. Afin d'évaluer l'effet de l'hétérogénéité spatiale de la mortalité due à la pêche sur le rendement, nous avons construit des modèles structurés d'après l'âge qui permettent diverses intensités de pêche dans trois régions à l'intérieur des frontières d'un stock et qui explorent des présuppositions de rechange concernant le stade du cycle pendant lequel a lieu la compensation de densité-dépendance. Si le taux de mortalité dû à la pêche (F) n'est pas excessif (c'est-à-dire si $F \leq F_{\mathrm{MSY}}$ défini pour le cas d'homogénéité spatiale), les simulations montrent qu'une variation spatiale de faible à modérée de l'intensité de la pêche n'affecte pas le rendement soutenable. Cependant, si la mortalité due à la pêche est excessive ($F > F_{\mathrm{MSY}}$), la variation spatiale de l'intensité de la pêche améliore souvent le rendement et peut de fait produire des rendements supérieurs au rendement soutenable maximal lorsque la compensation se fait après la dispersion et que le taux de recrutement dépendant de la densité est fonction de la densité locale des adultes. Le rendement additionnel produit dans ces simulations par la densité-dépendance après la dispersion est due au bas niveau de mortalité compensatoire dans les zones de pêche intensive, ainsi qu'à la dispersion dans ces zones de propagules provenant des zones avoisinantes peu exploitées.

[Traduit par la Rédaction]

Introduction

Most fisheries population models make the simplifying homogeneity assumption that spatial distributions of both the fish and the fishery are either well mixed or are spatially congruent (Walters and Martell 2004). The obvious appeal of this rather sweeping assumption is that spatial stratification and accounting of vital rates are not required (Hilborn and Walters 1992). This assumption might be largely valid for highly mobile pelagic species that do not exhibit site fidelity and persistent spatial stock structure. On the other hand, many demersal marine fish and invertebrate populations clearly violate this well-mixed, homogeneous assumption. A more appropriate description of many demersal populations may be a marine metapopulation (sensu Kritzer and Sale 2004), which is composed of subpopulations inhabiting discrete regions that are connected to one another by larval dispersal. Consideration of marine metapopulations in the ecological literature has generally focused on the issue of population persistence (Botsford et al. 2001; Armsworth 2002; Hastings and Botsford 2006). Much less is known about the effect of spatial variability in the distribution of fish (and fishermen) on catch. In particular, little attention has been given to the specific effect of spatial variation in fishing effort, or fishing mortality, on total sustainable yield. This becomes an important issue to consider when concerns about localized stock depletions and (or) surpluses have a substantial influence on policy and management.

As with most other research questions in fisheries biology, Beverton and Holt (1957) first gave consideration to the case where portions of a stock were subjected to differing levels of fishing intensity. They provided methods for estimating

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the overall fishing mortality coefficient (i.e., the weighted mean of fishing mortalities in constituent areas) and the overall fishing intensity from yield and abundance data. Using some of the theory presented in Beverton and Holt, Hart (2001) demonstrated how yield per recruit (YPR) is affected by variability in fishing mortality risks among individuals. A conclusion of Hart's (2001) analysis was that variability in fishing mortality risks within a stock generally led to decreases in YPR, with the largest decreases occurring near the homogeneous fishing mortality rate (F) that maximized YPR (F_{MAX}). While providing a starting point for understanding how spatial variability in fishing mortality risks will affect yield, it is not clear how these results would translate to dynamic models, with a defined relationship between spawning stock and recruitment, and more complex connectivity assumptions. Others have examined the problem from a different perspective by constructing models that describe fleet dynamics coupled with stock dynamics (e.g., Caddy 1975; Holland and Sutinen 1999; Sanchirico and Wilen 1999). Studies like these are useful in developing an understanding of the patterns and causes of geographic variability in fishing activity, yet it can be difficult to discern generalities about how spatial structure in fishing affects total yield.

More recent attention has been given to spatial management in fisheries biology from the perspective of marine reserves. Reserves are perhaps the extreme manifestation of spatially heterogeneous fishing activity, as a certain proportion of the total area inhabited by a stock experiences an F of zero. Investigations by Polacheck (1990) and DeMartini (1993) demonstrated that reserves generally decrease YPR, except for stocks experiencing heavy overfishing (see also Beverton and Holt 1957). This result also appears to hold when yield, rather than YPR, is calculated from dynamic models (Quinn et al. 1993; Botsford et al. 2004; Hart 2006). Hastings and Botsford (1999) showed that reserves and more conventional effort controls could result in mathematically equivalent yields when areas open to the fishery were subjected to infinite fishing mortality. Finally, Gaylord et al. (2005) demonstrated that fisheries with reserves can provide yields greater than conventional, effort-based management under a variety of conditions, but most notably when their models incorporated postsettlement density dependence. The variation in these results with regard to reserves and fishery yield appears to be model dependent.

When considering a spatially subdivided stock with connectivity between subpopulations, the life stage at which density-dependent compensation occurs becomes crucial to results. It is no longer possible to assume, as with most stock assessment models, that density dependence occurs at any time between the egg and the recruit stage. As a result, in this study we consider three manifestations of density dependence that are possible for fish populations and documented in the literature (Rose et al. 2001; Hixon and Webster 2002). First, we consider intrachohort density dependence, where the degree of compensation depends on the amount of pooled reproduction produced by adults in all substocks comprising the population. We then consider predispersal density dependence, where the degree of compensation is a function of the local (i.e., at the level of the substock) reproductive output, prior to dispersal. We finally consider postdispersal density dependence, where the degree of compensation has dependence on the local abundance of adults, which settling juveniles encounter after dispersal. The specific formulation and justification of these forms of density dependence are further detailed in the Materials and methods section and in Fig. 1.

The goal of this paper is to explore the effect of spatial variation in fishing effort and total potential yield. Our approach differs from previous studies of spatial variability in fishing mortality in that (*i*) we consider three alternative, hypothetical scenarios for the manner in which density-dependent mortality occurs; (*ii*) we consider marine reserves as an extreme, special case along a spectrum of spatial heterogeneity in F and explicitly consider more modest variability in fishing activity; and (*iii*) we specify the degree of spatial variation in F as a control variable rather than the fraction of area in reserves. In addition, we consider a simple example where spatial variation in fishing effort also has a temporal component (i.e., serial geographic expansion of a fishery), and we evaluate its effect on yield. Our results reveal the fishery conditions having the potential to increase or decrease yields, compared with the well-mixed, spatially homogeneous case, and help to explain the diversity of results obtained on this subject to date.

Materials and methods

We used standard fisheries equations in deterministic, age-structured models to calculate yield under different assumptions of spatially heterogeneous fishing mortality and density-dependent recruitment. We first consider a conventional model, assuming that the fishery operates in one well-mixed region and that F is constant over space and time. The maximum sustainable yield (MSY) and the equilibrium yield obtained at different levels of F are calculated from this base model. We then consider models where the stock is spatially divided into three, equal-area subpopulations and perform the same yield calculations. However, as spatially structured fishing mortality is added to the base model, assumptions regarding the life stage at which density dependence operates become central to our results. We begin by describing the base model in more detail. We then describe three alternative, spatially structured models, from which yields are compared with the more typical, nonspatial formulation.

Base model

The construction of the base model and the selection of specific parameter values were chosen to represent a relatively productive northeast Pacific rockfish (*Sebastes* sp.) population (Table 1). The model is discrete with an annual time step and contains 20 age categories, the oldest being an accumulator group (all individuals ≥20 years). Maturity is assumed to be a logistic function of age:

$$(1)\qquad P_a = \frac{1}{1 + \exp[-m(a - b)]}$$

where P_a is the proportion of individuals mature at age a, m determines the rate of maturation, and b is the age at 50% maturity. Additionally, we assume that fishery selectivity is a logistic function of age, following eq. 1, with the exception

Table 1. Parameter set for the model population.

Parameter	Symbol	Value
von Bertalanffy asymptotic length	L_∞	50
von Bertalanffy growth coefficient	k	0.25
von Bertalanffy length at age zero	t_0	0
Length–biomass coefficient	c	1×10^{-5}
Length–biomass exponent	d	3
Fecundity coefficient	α	200
Age at 50% maturity	b	6
Curvature parameter for maturity	m	1
Age at 50% fishery selectivity	s_1	5
Curvature parameter for fishery selectivity	s_2	1.5
Natural mortality rate	M	0.25
Stock–recruitment steepness	h	0.7
Stock–recruitment maximum recruitment	R_0	1000
Unfished reproduction per recruit	ϕ	204 436

that selectivity parameters s_1 and s_2 substitute for parameters m and b, respectively, and S_a replaces P_a and represents the proportion of the full fishing mortality rate experienced by fish age a. In this hypothetical population, individuals are recruited to the fishing gear before they mature (i.e., fishery selectivity is 50% at age 5 years), while 50% of females are mature at age 6 years. Individuals grow in length according to the von Bertalanffy growth model, and individual weight is a power function of length ($W_a = cL_a^d$), where W_a is biomass at age a, L_a is length at age a, and c and d are length–weight parameters. Finally, egg production for an individual of age a (E_a) is proportional to weight, $E_a = \alpha W_a$, with α effectively representing weight-specific fecundity.

The density-dependent dynamics of the population are driven by the Mace and Doonan (1988) parameterization of the Beverton–Holt stock–recruitment relationship:

$$(2)\qquad R = \frac{0.8R_0hS}{0.2\phi R_0(1-h)+(h-0.2)S}$$

R_0 represents the recruitment expected from an unfished stock, and ϕ is the unfished reproduction per recruit (prior to compensation). The steepness parameter (h) is the proportion of unfished recruitment that results when the spawning stock is reduced to 20% of the unfished level. Steepness can vary from 0.2 (linear relationship between egg production and recruitment) to 1.0 (recruitment does not change with changes in spawning stock size). In eq. 2, we keep the notation conventions of S representing a measure of the stock (e.g., egg production) and R representing recruits. However, for the spatial models developed in the next section, we let the S and R notation represent general measures of abundance before and after density-dependent compensation, as density dependence could occur between different stage transitions.

Yield biomass is calculated at time t (Y_t) by taking the product of the fraction of individuals at each age that die because of fishing, abundance ($N_{a,t}$), and biomass (W_a), summed over all ages:

$$(3)\qquad Y_t = \sum_a \left(\frac{S_aF}{M+S_aF}\{1-\exp[-(M+S_aF)]\}\right)N_{a,t}W_a$$

The large term in parentheses is the Baranov catch equation with a separability modification to allow for a non-knife-edged selectivity schedule (Deriso et al. 1985); M denotes the natural mortality rate. Equilibrium yield is obtained by running the model forward with a constant F for a sufficient number of years to allow for yield convergence.

Spatial model 1: intracohort density dependence

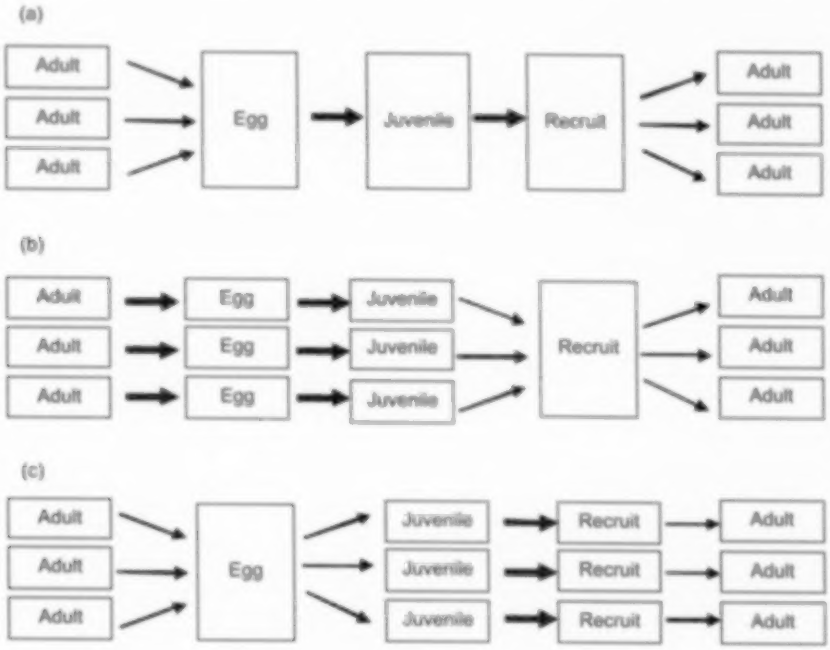
As with all the spatial models considered in this paper, the total stock is divided into three equal regions. We assume that the regions have equivalent productivity and are distinct, such that there is no exchange of adults among regions. Population connectivity among the three regions only occurs through dispersal prior to recruitment.

For the intracohort density dependence model, compensation occurs on the pooled reproduction of the three constituent regions (Fig. 1*a*). Note that the aggregate egg (or juvenile) production from all regions forms a pool, from which the number of age-1 recruits is determined according the Beverton–Holt spawner–recruit relationship (eq. 2). The recruit pool is then equally redistributed back to the three regions. Here, the level of density-dependent compensation is determined by the aggregate level of spawning summed over the three regions. The model dynamics are equivalent whether the density-dependent transformation occurs between the egg and juvenile or the juvenile and recruit stages. The mechanisms causing this type of compensation can be direct, such that mortality rates on eggs and juveniles increase with their density (Cowan et al. 2000). Indirect density-dependent mortality in larval fish can arise because of density-dependent larval growth, which in turn extends the high-mortality larval stage and results in density-dependent mortality (Shepherd and Cushing 1980; Houde 1987, 1989). While variability in growth rate can be common for larval fishes, demonstrating that such variation has a density-dependent component has proven elusive (Cowan et al. 2000). This model could also apply to a population that experiences density-dependent mortality after settlement, but with the degree of compensation due to the number of incoming propagules and not to the abundance of the standing stock (as in the postdispersal density dependence model). An example of this form of density dependence is the increased mortality rates for larger year classes of blue rockfish (*Sebastes mystinus*) in their first year after settlement (Adams and Howard 1996).

Spatial model 2: predispersal, intercohort density dependence

For the predispersal density dependence model, the spawner–recruit relationship is applied at the local, regional scale prior to dispersal, rather than on the pool of reproductive output aggregated from all three regions (Fig. 1*b*). To do this, we apply the Beverton–Holt equation with a modified R_0 parameter to reflect that each constituent region is one-third of the total area inhabited by the stock. As such, R_0 in each of the three regions is 1000 ÷ 3, rather than 1000 as in the base and intracohort density dependence models. Following density-dependent compensation, individuals are then

Fig. 1. Schematic representations of the (*a*) intracohort, (*b*) predispersal intercohort, and (*c*) postdispersal intercohort density dependence models. In each model, the adult stock resides in the three nonoverlapping regions. We denote the life history transitions in which density dependence can operate with a heavy arrow. In each model, density dependence only operates during one stage transition. However, there are two mathematically equivalent stage transitions for the intracohort and predispersal models, both identified by the heavy arrows.



aggregated and equally redistributed back to the three regions. A plausible mechanism that could lead to this type of compensation is the case where egg production depends on the local density of spawners. This has been documented for east Tasmanian orange roughy (*Hoplostethus atlanticus*), where mean individual fecundity increased significantly during a 5-year period when the estimated stock size was decreased by approximately one-half (Koslow et al. 1995). Another mechanism that could lead to this type of compensatory response is when adult somatic growth (and thus reproductive output) depends on the local density of spawners. This scenario is not explicitly depicted in Fig. 1*b*, but is implicit with processes underlying the model's formulation. Lorenzen and Enberg (2002) found evidence for decreasing asymptotic length with increasing population biomass for 9 of the 16 fish populations they considered.

Spatial model 3: postdispersal, intercohort density dependence

The postdispersal density dependence model assumes that equal numbers of propagules are redistributed to each of the three constituent regions and that compensation depends on local processes following dispersal (Fig. 1*c*). Here, each region produces a certain number of eggs (or equivalently, juveniles), which are aggregated into a pool. The propagules are then redistributed equally among the three regions, without compensation having yet occurred. Density dependence is then applied by multiplying the predicted recruits per spawner by the equally redistributed reproductive output:

$$R_i = (\tilde{R}_i / S_i)(S_{\text{total}} / 3) \tag{4}$$

Here, $\tilde{R}_i$ is the number of recruits predicted from the Beverton–Holt function in each of three regions i, given the spawning stock size in that region (S_i). S_{total} is the pooled reproductive output from adults in the three constituent regions, and R_i is the realized number of recruits added to the population in region i. This formulation allows for the level of compensation to be a function of local adult density. Also, because the number of settlers is equal in each region, but the $\tilde{R}_i/S_i$ ratio potentially differs in each region because of variability in F, the distribution of recruits is not the same among regions. This is the only model formulation of the three considered here that results in unequal age-1 recruitment among the three regions. There is perhaps the most evidence from empirical studies of the presence of density-dependent regulation of fish populations between the stages of settlement and recruitment to the fishery (reviewed by Caley et al. 1996; Hixon and Webster 2002). Per-capita mortality on newly settled rockfishes was found to be density dependent in the presence of predators, but density independent when predators were excluded from enclosures (Johnson 2006). Other studies have detected postdispersal density dependence over larger spatial areas and durations. Myers and Cadigan (1993) found high levels of density-dependent mortality occurring for 17 stocks of Atlantic demersal fishes, measured between settlement and age-2. Here, juvenile mortality was related to both the abundance within a cohort, which is represented in this paper as the intracohort density dependence model, and the abundance of the previous year's cohort, which is described best by this model. Using similar methods on long time series (44–73 years), Fromentin et al. (2001) detected the presence of both intracohort and delayed density-dependent mortality for juvenile Norwegian cod (*Gadus morhua*), though the strength varied by region. While we considered the case where the degree of compensation is determined by the biomass of resident conspecifics (i.e., cannibalism), we acknowledge that postsettlement mortality can be a function of other predators in the community (see also cultivation–depensation effects described by Walters and Kitchell 2001), but do not take multispecies interactions into account here.

Spatial heterogeneity in fishing

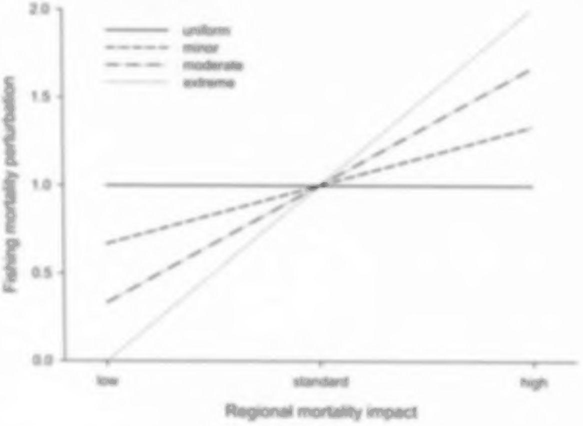
We considered a spectrum of different levels of spatial heterogeneity in F, in addition to the default case in which F is homogeneous among the three modeled regions (Fig. 2). In the uniform case, the instantaneous fishing mortality was made equal in all three regions, and the summed yield was therefore the same as the nonspatial base model. Minor spatial heterogeneity in fishing intensity was modeled by reducing the fishing mortality rate by a factor of 0.33 in what will be called the low impact area and concomitantly increasing the F by a factor of 0.33 in a high impact area, resulting in no net change in fishing pressure over all three areas. This is equivalent to shifting one-third of the fishing effort that had previously occurred in one area to another. Similarly, moderate heterogeneity in fishing was modeled by perturbing fishing mortalities by $\pm 0.67F$ in the high and low impact areas, whereas extreme heterogeneity was modeled by a perturbation of $\pm 1.00F$. The latter scenario effectively doubled the fishing mortality in the high-impact region and created a marine reserve in the low-impact region (i.e., $F = 0$). Note that in all scenarios, mortality perturbations in the high- and low-impact areas were relative to that implemented in the standard area. For the remainder of this paper, we consider these four perturbation scenarios for F levels ranging from 0.05 to 1.0.

MSY and F_{MSY} are both sensitive to the choice of M and steepness. We used an h value of 0.7 in the base model, as it is plausible for a productive Pacific rockfish (Dorn 2002). The base M used was 0.25 year^{-1}, similar to *Sebastes jordani* (Ralston et al. 2003). However, to evaluate if our results were robust to alternative life histories, we calculated yield curves for values of M and h above and below the values used in our hypothetical population, for each of the three density dependence scenarios considered. Equilibrium yield was calculated as a function of F for the three models under the four spatial fishing scenarios for M of 0.15 and 0.35. Yield curves were also calculated in the same manner for $h = 0.5$ (a less resilient population) and $h = 0.9$ (a highly resilient population).

Serial depletion

All calculations of yield up to this point were made at equilibrium. Yet, fishery systems are usually not at equilibrium, especially during early developmental periods. Moreover, a common pattern in fishery development is the sequential or serial depletion of fishing regions, whereby effort and fishing mortality progress sequentially over space. To better understand the yield characteristics of this situation, we model two serial depletion scenarios by allowing regional F to increase linearly from a low equilibrium value of $F = 0.10$ to a level approximately 50% greater than F_{MSY}. Once F reaches this highest level, F decreases linearly to F_{MSY} where it then remains constant. We consider this regional pattern of F increasing, decreasing, and then settling at F_{MSY} occurring for the three regions sequentially, with two lag times of fishery spread. For the fast depletion scenario, we increased F for each region with a lag of 3 years (i.e., linear increase in F for region 2 occurs 3 years after the initiation of increased F in region 1), leading to all regions converging at F_{MSY} after 16 years. For the slow serial depletion scenario, we increased F for each region with a lag of 11 years, with all regions converging at F_{MSY} after 49 years. Both the fast and slow serial depletion scenarios result in the average, system-wide F increasing over time to a level above F_{MSY}, then decreasing to, and settling at, F_{MSY}. Total yield, summed over the three regions, was then calculated at each time step for the three alternative density-dependent models.

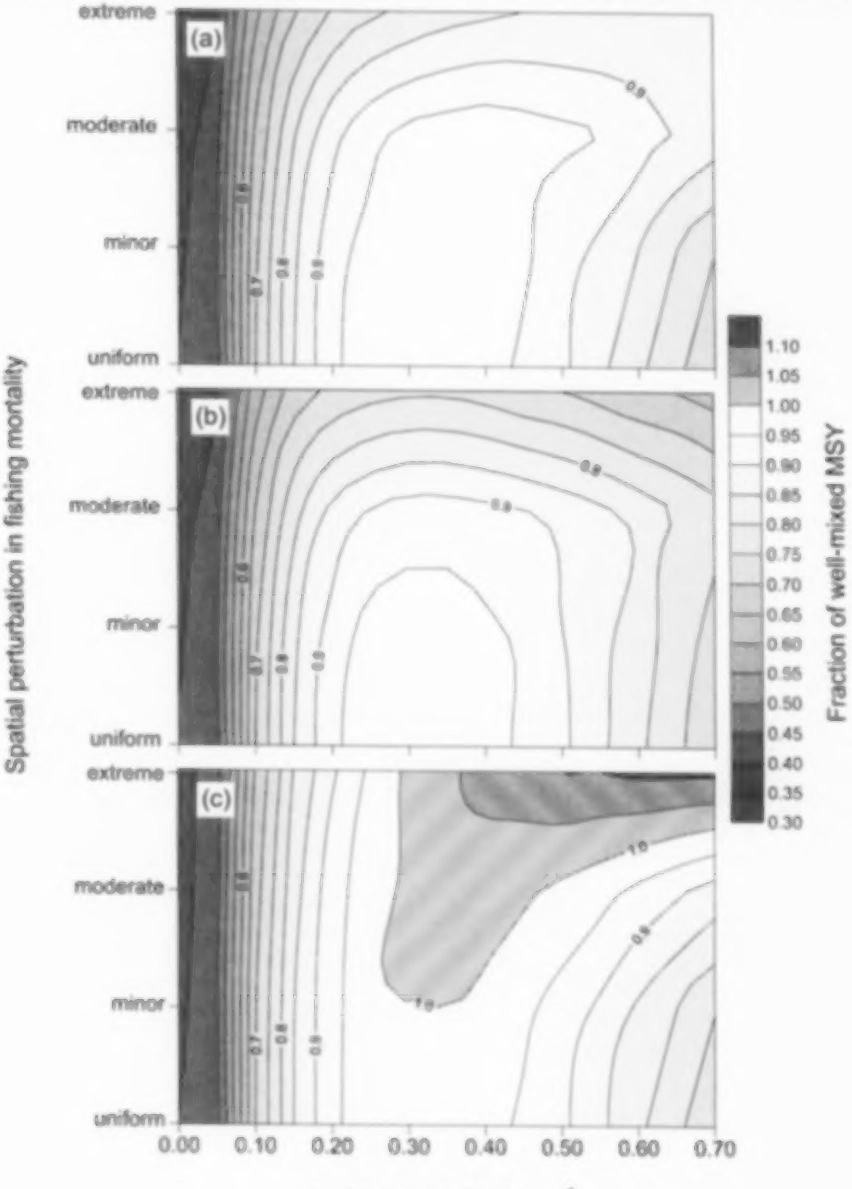
Fig. 2. The degree to which spatial perturbations in fishing mortality (F) were assumed over regions subjected to low, standard, and high levels of fishing. Uniform (solid line) fishing mortality perturbation denotes a constant level of F across the three regions. Minor (dashed line) and moderate (dash-dot line) perturbations vary F by a factor of ±0.33 and ±0.67, respectively, from the level of F in the standard region. The extreme fishing mortality perturbation (dotted line) results in the low region becoming a no-take reserve and the high region experiencing twice the F of the standard region.



Results

The effect of spatial heterogeneity in fishing on yield depended on (*i*) the manner in which density dependence in the population is expressed, (*ii*) the amount of spatial heterogeneity in F, and (*iii*) the overall mean value of F (Fig. 3). The three hypothetical compensation scenarios are shown as individual contour plots (Fig. 3), with the independent variables corresponding to the instantaneous F and the extent of spatial perturbation in fishing. The contours represent real-

Fig. 3. Yield contours for the (*a*) intracohort, (*b*) predispersal, and (*c*) postdispersal density dependence models, calculated as a function of the instantaneous fishing mortality rate (*F*) and the degree of spatial perturbation in *F*. Yield is summed over the three spatial regions and is normalized to the maximum sustainable yield (MSY) obtained for the single, well-mixed population model.



ized sustainable yield as a fraction of MSY from the base, nonspatial model.

For the homogeneous *F* case (i.e., uniform mortality perturbation), all models converge to the same yield solution. Predictably, this yield curve is identical to the yield curve of the base model that assumes a single, well-mixed population and makes no assumptions about the manner in which density dependence operates. In the base model (as parameterized in Table 1), MSY = 91.2 mt·year^{-1} and F_{MSY} = 0.309 year^{-1}.

For the intracohort and predispersal density dependence models (Figs. 3*a* and 3*b*), all forms of spatial variability in *F* resulted in yield levels below the single population MSY (realized fraction of global MSY < 1.00). In contrast, equilibrium yields greater than the single population MSY were obtained for the postdispersal density dependence model,

Table 2. Sensitivity of yield to levels of steepness (*h*) below (0.5) and above (0.9) the level assumed in other analyses (0.7), expressed as the proportion of the well-mixed yield.

		Spatial variation in fishing								
		Minor			Moderate			Extreme		
F	Well-mixed yield	I	PRE	POST	I	PRE	POST	I	PRE	POST
***h* = 0.5**										
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.1	56.00	0.99	0.98	0.99	0.94	0.93	0.97	0.86	0.83	0.94
0.2	62.48	1.00	0.99	**1.01**	0.99	0.95	**1.02**	0.92	0.82	**1.02**
0.3	51.11	1.04	1.02	1.03	1.13	1.03	1.13	1.14	0.93	**1.25**
0.4	34.87	1.10	1.07	1.08	1.40	1.23	1.34	1.65	1.23	1.74
0.5	20.62	1.19	1.14	1.16	1.85	1.58	1.71	2.71	1.87	2.75
0.6	10.95	1.29	1.24	1.25	2.60	2.16	2.31	4.95	3.19	4.83
0.7	5.45	1.41	1.35	1.36	3.72	3.05	3.22	9.67	5.90	9.10
0.8	2.64	1.53	1.47	1.47	5.30	4.32	4.51	19.48	11.33	17.70
0.9	1.27	1.64	1.58	1.58	7.39	6.02	6.21	39.46	22.06	34.76
1	0.62	1.74	1.68	1.68	10.02	8.18	8.37	79.16	42.79	67.78
***h* = 0.9**										
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.1	67.23	0.98	0.98	0.99	0.93	0.92	0.97	0.82	0.82	0.93
0.2	96.10	0.98	0.98	1.00	0.91	0.91	0.98	0.76	0.75	0.94
0.3	109.80	0.98	0.98	1.00	0.92	0.91	0.99	0.74	0.72	0.97
0.4	116.39	0.99	0.98	1.00	0.93	0.91	1.01	0.73	0.70	1.01
0.5	119.23	0.99	0.98	**1.01**	0.94	0.92	**1.02**	0.73	0.69	**1.04**
0.6	119.96	0.99	0.99	**1.01**	0.96	0.93	**1.04**	0.74	0.69	**1.09**
0.7	119.42	1.00	0.99	**1.01**	0.97	0.94	**1.05**	0.74	0.68	**1.14**
0.8	118.10	1.00	0.99	1.01	0.99	0.95	**1.07**	0.75	0.68	**1.19**
0.9	116.27	1.01	0.99	1.02	1.00	0.96	**1.08**	0.77	0.68	**1.24**
1	114.13	1.01	1.00	1.02	1.02	0.96	**1.09**	0.78	0.68	**1.29**

Note: Bold values indicate when yields exceed the global maximum sustainable yield of the well-mixed model. Well-mixed yeild refers to the equilibrium yield at each level of fishing mortality rate (*F*). I, intracohort density dependence model; PRE, predispersal density dependence model; POST, postdispersal density dependence model.

with the greatest yields occurring with a combination of high average *F* and the greatest spatial perturbation in *F* (i.e., reserves; Fig. 3c). In the postdispersal density dependence model, when fishing in the high impact area was doubled and in the low impact area was zero, the global MSY exceeded the single area model MSY by 11.5%. In Fig. 3, note that because of interpolation by the smoothing algorithm (Golden Software 1999), the 1.0 contour interval (100% of base case MSY) approaches but does not intersect the *x* axis at $F = 0.309\ \text{year}^{-1}$, as it should.

While yields greater than the well-mixed MSY were only obtained with the postdispersal density dependence model, spatial variation in *F* can result in equilibrium yields that either exceed, or are less than, the well-mixed equilibrium yield (Fig. 3). For all three models, increasing spatial heterogeneity in *F* resulted in a shift in F_{MSY} to a higher value and a less pronounced descending limb of the yield curve at high *F*. The shift of F_{MSY} to a higher value and the flattening of the yield curve at higher levels of spatial variability in *F* resulted in decreased equilibrium yields (relative to the well-mixed case) at low *F*, but a modest increase in equilibrium yield at very high *F*. The decreased equilibrium yields at lower levels of *F* and high spatial heterogeneity are most severe for the intracohort and predispersal density dependence models. Finally, if we again consider fishing mortality rates greater than F_{MSY}, it appears that in the intracohort model, and to a lesser extent the predispersal density dependence model, the highest yields occur at some intermediate level of spatial heterogeneity in *F*. In contrast, the postdispersal density dependence model provides the highest yields as spatial heterogeneity increases to the extreme, reserve case. This result is somewhat dependent on the size of the reserve area assumed in the model. The increase in yield at moderate levels of spatial heterogeneity in *F* is diminished if we consider smaller reserve areas (e.g., 10% or 20% of the total area; data not shown).

The generality of these results extends to populations with different life history parameters. How yield is affected by steepness values below (0.5) and above (0.9) the assumed level in the base model (0.7) is demonstrated (Table 2). For both steepness values considered in Table 2, yields exceeding the global, well-mixed population MSY only occur for the postdispersal density dependence model, though the potential increases were very small and occur at a narrow range of *F* in the less productive population ($h = 0.5$). For this low-productivity case, given a fixed level of fishing mortality, local gains in equilibrium yield were observed at high *F* with increasing spatial heterogeneity in fishing effort. Note that unlike the data presented in Fig. 3, which are expressed relative to the global MSY, the elements presented in

Table 3. Sensitivity of yield to levels of natural mortality rate (*M*) levels below (0.15) and above (0.35) the level assumed in other analyses (0.25), expressed as the proportion of the well-mixed yield.

		Spatial variation in fishing								
		Minor			Moderate			Extreme		
F	Well-mixed yield	I	PRE	POST	I	PRE	POST	I	PRE	POST
***M* = 0.15**										
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.1	144.59	0.98	0.98	0.99	0.92	0.91	0.98	0.80	0.77	0.94
0.2	161.57	1.00	0.98	**1.01**	0.97	0.92	**1.02**	0.82	0.73	**1.03**
0.3	144.05	1.02	1.00	1.02	1.06	0.96	1.10	0.93	0.75	**1.20**
0.4	115.07	1.06	1.02	1.05	1.22	1.06	1.22	1.15	0.84	**1.51**
0.5	83.75	1.12	1.07	1.10	1.48	1.22	1.42	1.55	1.04	**2.05**
0.6	55.48	1.21	1.14	1.17	1.91	1.52	1.76	2.29	1.43	**3.03**
0.7	33.55	1.32	1.24	1.26	2.61	2.01	2.31	3.72	2.18	**4.90**
0.8	18.81	1.45	1.36	1.38	3.73	2.81	3.18	6.51	3.61	8.53
0.9	10.01	1.59	1.49	1.51	5.46	4.05	4.49	12.03	6.38	15.67
1	5.18	1.73	1.62	1.64	7.97	5.86	6.38	22.85	11.66	29.60
***M* = 0.35**										
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.1	30.82	0.99	0.98	0.99	0.94	0.94	0.97	0.86	0.85	0.94
0.2	45.67	0.98	0.98	0.99	0.93	0.92	0.97	0.81	0.79	0.94
0.3	52.80	0.99	0.98	1.00	0.94	0.91	0.99	0.80	0.76	0.96
0.4	55.76	0.99	0.98	1.00	0.95	0.92	1.00	0.81	0.75	1.00
0.5	56.28	1.00	0.99	1.01	0.98	0.93	**1.03**	0.84	0.75	**1.04**
0.6	55.32	1.01	0.99	1.01	1.00	0.95	**1.05**	0.87	0.76	**1.10**
0.7	53.41	1.01	1.00	1.02	1.04	0.97	**1.08**	0.92	0.77	**1.17**
0.8	50.88	1.02	1.00	1.03	1.07	0.99	1.11	0.97	0.80	**1.25**
0.9	47.96	1.03	1.01	1.03	1.12	1.02	1.14	1.03	0.82	**1.34**
1	44.78	1.04	1.02	1.04	1.16	1.05	1.18	1.11	0.86	**1.45**

Note: Bold values indicate when yields exceed the global maximum sustainable yield of the well-mixed model. Well-mixed yeild refers to the equilibrium yield at each level of fishing mortality rate (*F*). I, intracohort density dependence model; PRE, predispersal density dependence model; POST, postdispersal density dependence model.

Table 2 are expressed relative to the local sustainable yield conditional on *F*. For the $h = 0.5$ case, the reserve spatial perturbation provides the largest gain in equilibrium yield over the well-mixed scenario. In contrast, for the high-productivity case ($h = 0.9$), at high levels of fishing mortality, increasing spatial heterogeneity in *F* has a negative effect on local equilibrium yield, except for the postdispersal density dependence model.

Similar conclusions were drawn from considering *M* levels bracketing the value used in the base population model (Table 3). It is worth noting again that yields exceeding the single population MSY are only obtainable with the postdispersal density dependence model, with some degree of variability in *F* over space, regardless of the different *h* and *M* values considered. The largest effect of changing *h* or *M* values is the associated shifts in F_{MSY} that occur with such a change. However, the qualitative effects on yield for the three different forms of density dependence employed in the models remain quite similar.

The postdispersal density dependence model also produces the highest yields relative to both the intracohort and predispersal models when *F* varies over both space and time (Fig. 4). For a fast serial depletion scenario, yield increased similarly in each of the three density dependence models for approximately the first 10 years. However, yields from the postdispersal density dependence model exceeded the larval and spawner density dependence models from approximately years 10 through 45, though these increases were quite modest (Fig. 4*c*). If we allow for sequential depletion of regions to proceed at a slower pace, the postdispersal density dependence model was again able to produce yields greater than the intracohort and predispersal density dependence models relatively early in the time series (approximately years 10–30). This yield premium from the postdispersal density dependence model disappeared after approximately 30 years, when all three regions were being fished at rates higher than F_{MSY} for the system (Fig. 4*f*). In addition, the prolonged serial depletion scenario we present here results in yield dipping below the single population MSY level for a short period of time, after all regions have experienced high fishing mortality rates. Yields approach the MSY equilibrium in all three models at approximately year 60.

To understand why the postdispersal density dependence model consistently produced the greatest yields when *F* showed substantial spatial variation, we examined how per-region, equilibrium recruitment and biomass-weighted fishing intensity (total yield divided by the total exploitable biomass) varied among the three models and present representative results from the $F = 0.5$ case (Fig. 5). Equilibrium

Fig. 4. Time series of fishing mortality rate (*F*), the *F* averaged over space, and yield for a fast (*a–c*) and slow (*d–f*) serial depletion scenario. Plots (*a*) and (*d*) depict the region-specific variation in *F* over time. Plots (*b*) and (*e*) display the average *F* over time. Yields from the intracohort (solid black line), predispersal (dotted line), and postdispersal density dependence models (dashed line) are shown in plots (*c*) and (*f*). The gray horizontal line depicts the maximum sustainable yield in the spatially uniform *F* case.

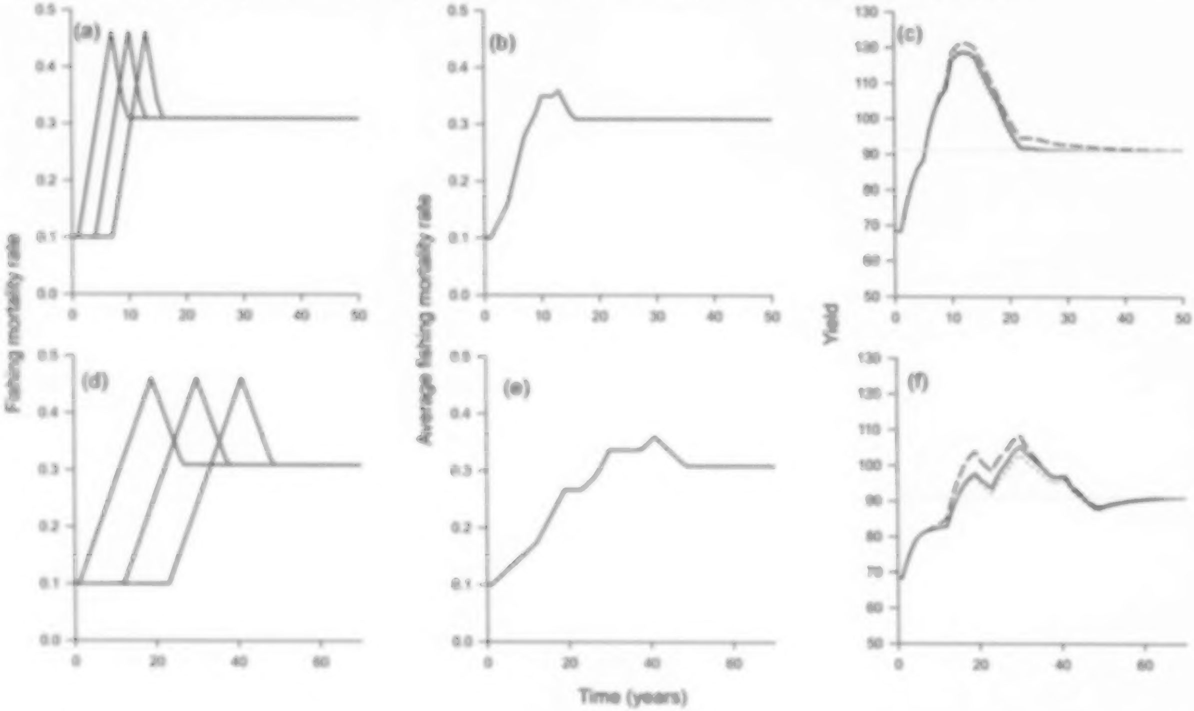
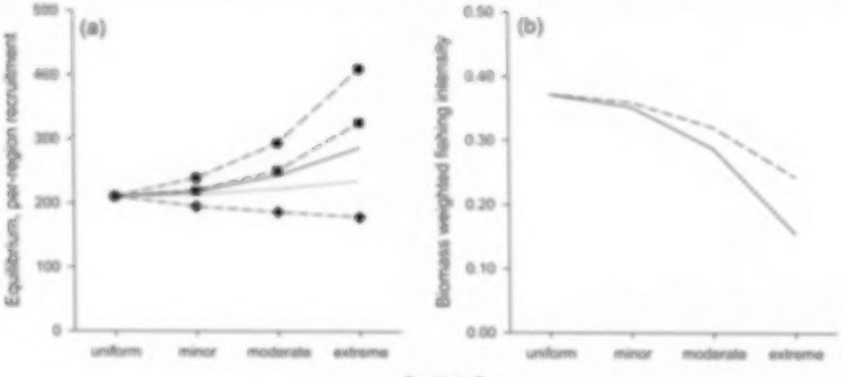


Fig. 5. Equilibrium and per-region recruitment (*a*) and the biomass-weighted fishing intensity (*b*) for four spatial fishing scenarios, calculated at an average fishing mortality rate (*F*) of 0.50. Recruitment for the intracohort (solid line) and predispersal (dotted line) density dependence models is equivalent in all three regions. Recruitment for the postdispersal density dependence model varies among regions when there is spatial variability in *F*. Dashed lines with diamonds denote the low or zero *F* region, squares denote the region fished at the mean *F*, and circles denote the region fished at the high level of *F*. The biomass-weighted fishing intensity for the three models uses the same line styles as in (*a*), with exception that the postdispersal model is denoted by a simple dashed line. Note that the biomass-weighted fishing intensity is equivalent for the intracohort and predispersal density dependence models.



recruitment was equivalent for all three models when fishing mortality is evenly distributed over space. As spatial heterogeneity in *F* increases, equilibrium and per-region recruitment increases for both the intracohort and predispersal density dependence models, though the increases are smaller in the predispersal density dependence case (Fig. 5*a*). For the postdispersal density dependence model, recruitment differs among regions as spatial heterogeneity in *F* is introduced. In particular, recruitment in the regions experiencing the standard and high levels of *F* receive the greatest level of equilibrium recruitment, while the region experiencing low or zero *F* receives fewer recruits. Since recruitment in heavily fished regions is largely decoupled from local spawning production in the postdispersal density dependence model, high levels of recruitment occur despite heavy fishing and low levels of spawning. The low spawning stock in heavily fished areas produces a high per-capita recruitment rate ($\bar{R}_i/S_i$), which is multiplied by high levels of spawning redistributed from the lightly fished (or reserve) areas, resulting in large equilibrium recruitment in heavily fished areas. This combination of high equilibrium recruitment, in regions with high *F*, for the postdispersal density dependence model resulted in an increased biomass-weighted fishing intensity relative to the other models (Fig. 5*b*). It is this relatively greater biomass-weighted fishing intensity that allows the postdispersal density dependence model to produce yields greater than the larval and spawner density dependence models under the array of conditions we explored.

Discussion

Geographical variation in fishing intensity is likely to be the rule, rather than the exception, for most stocks. Using deterministic models with simplified assumptions about larval connectivity, we find that the life history stage and spatial scale at which density dependence operates become central to understanding how yield responds to spatial variation in fishing.

If a stock is not overfished (i.e., $F \le F_{\mathrm{MSY}}$), little loss in yield is incurred when fishing varies spatially. We conclude that in well-managed fisheries that effectively control the total amount of fishing effort, a spatial mosaic of localized depletions and surpluses within the range of a stock is not of particular concern to optimization of total yield; much more important is to control the total amount of fishing.

When fishing mortality is excessive ($F > F_{\mathrm{MSY}}$), some degree of spatial variation in fishing intensity can actually improve yields over the homogeneous base case. In particular, a combination of postdispersal density dependence, spatial heterogeneity in *F*, and high levels of average *F* can lead to increased yields above the well-mixed, uniform fishing mortality case. These same conditions resulted in yields greater than those produced by the intracohort and predispersal density dependence models in idealized serial depletion scenarios. The mechanism that allows for the postdispersal density dependence model to produce greater yields relative to the other models appears to be the higher equilibrium recruitment levels in regions subjected to the greatest fishing mortality. This can happen when areas with low fishing mortality (e.g., reserves or refuge areas) donate propagules to heavily fished areas, and the settlers are subjected to low levels of compensatory mortality that occurs at low stock sizes. This results in a greater proportion of the overall stock becoming vulnerable to harvest and hence produces higher yields. Hart (2001) noted that spatial heterogeneity in *F* always leads to decreased levels of numbers and biomass-based exploitation rates, given equal levels of fishing effort. We can see this effect in Fig. 5*b*, where biomass-weighted fishing intensity decreases with the degree of spatial heterogeneity in *F* for the intracohort and predispersal models. This presumably leads to the decreased yields observed in these models with increased spatial variability in *F*. The specific formulation of the postdispersal density dependence model reduces this effect. Biomass-based fishing intensity still decreases with spatial variation in *F*, yet to a lesser degree.

Our results lend support to a number of previous studies, mostly from the marine reserve literature. First, we found that increasing spatial variability in *F* for the intracohort and predispersal density dependence models, especially for the case of reserves, can lead to decreased yield unless the stock is overfished (Gerber et al. 2003, and references therein). Second, spatial variation in *F* leads to decreased yields for nearly all levels of *F* in the predispersal density dependence model. This result is consistent with Gådmark et al. (2006), who demonstrated that yields could decrease with the implementation of reserves, because increased population biomass within reserves causes adverse, density-dependent effects on growth and reproductive processes. While this is not an explicit mechanism built into the models we use here, the predispersal density dependence model approximates this condition by assuming that recruits are a function of local egg production, which is a function of adult density and size. Third, a combination of spatial variability in *F*, postdispersal density dependence, and high levels of *F* can lead to greater yields than the spatially uniform fishing case, as demonstrated by Gaylord et al. (2005). It appears that the result of increased yields with postdispersal density dependence is somewhat robust to model details as we utilize more demographically realistic, fully age- and size-structured models, while the models used in Gaylord et al. (2005) are stage-structured. Additionally, their models utilize more realistic dispersal kernels to represent connectivity, while we assume equal redistribution of larvae; yet the conclusions are qualitatively similar. Finally, we find that any level of spatial variation in *F* leads to a flattening of the yield curve over the range of plausible levels of average *F*. This less dome-shaped yield curve, also noted by Apostolaki et al. (2002) for the case with reserves, may be an important hedge against assessment errors and allow the stock to be less prone to collapse because of overfishing. Even so, others have noted that for a number of reasons, marine reserves are likely to increase the imprecision of conventional stock assessments (Field et al. 2006; M.R. O'Farrell, L. Botsford, S. Ralston, and C.B. Grimes, unpublished data).

We made several simplifying assumptions to reduce model complexity and increase the generality of this analysis. For example, we assume that prerecruit propagules are redistributed uniformly among regions. This assumption may be unrealistic for populations exhibiting high levels of self-recruitment (Jones et al. 1999; Swearer et al. 1999). If connectivity among regions were vanishingly small, the yield dynamics would approach the uniform fishing case at the scale of the individual region. Under such a scenario, differences in yield would not depend on the stage at which density dependence operates. We also assumed that there was no postrecruitment movement between regions. This is plausible for reef fishes with low mobility, where suitable habitat is separated by unsuitable areas. Fishes with high levels of mobility would tend to wash out the spatial structure created by regional differences in fishing mortality. As a result, even if fishing mortality were heterogeneous over space, the yield dynamics would approach the uniform scenario, and again, the form of density dependence would likely be less important in determining yield. We assume that recruitment is only due to density-dependent effects and do not consider stochastic, density-independent mortality as a factor determining year class strength. Again, the differences in yield we observe among the three density-dependent models considered here would likely decrease as the strength of density-independent mortality relative to density-dependent effects increased. Finally, we do not consider spatial variation in productivity, though this is likely common for marine populations. Related to this, fishermen tend to aggregate at the most productive areas, where fishing success will likely be higher. These cases were not considered, but may be included for more specific applications.

In conclusion, we have described how spatial heterogeneity in F can lead to differences in yield from the spatially homogenous F case for three alternative models of density-dependent compensation. Historically, geographic differences in fishing mortality were likely more pronounced than in the present day, because of isolation of fishing areas that were too far away from ports to fish safely or economically (Pauly et al. 2002; Walters 2003). In such a system, natural reserves or harvest refugia would be maintained in areas that were expensive or dangerous to fish, while heavier fishing occurred nearer to ports. Increased technology and larger fishing vessels can effectively homogenize fishing mortality over a stock's range by allowing fishing in difficult regions under diverse conditions. However, current calls for management of fisheries with marine reserves would tend to move fisheries back toward more extreme spatial heterogeneity in F than likely exists today. The results we present here represent a first step toward understanding how such possible shifts will affect yield in both the long- and short-term future.

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Is gonadal investment in walleye (*Sander vitreus*) dependent on body lipid reserves? A multipopulation comparative analysis

Matthew D. Moles, Thomas A. Johnston, Beren W. Robinson, William C. Leggett, and John M. Casselman

Abstract: A key requirement of effective fisheries management is a better understanding of the mechanisms driving recruitment variability. Recent research suggests that the quantity and quality of gametes produced by fish is closely linked to the availability of surplus energy, usually stored as lipid. We sampled mature walleye (*Sander vitreus*) from seven populations across Canada to determine if indices of reproductive effort were positively related to indices of adult nutrient reserves, primarily body lipid concentration. Populations varied greatly in growth rates, body lipid contents, and reproductive traits. Within-population trends between indices of reproductive effort and parental body traits were highly variable. Body lipid concentration was most closely related to gonad lipid concentration, but not in all populations. Among populations, relative fecundity and ovary lipid concentrations were positively related, and egg size was negatively related to whole-body lipid concentrations; no trends were evident for males. Our results suggest that relationships between walleye reproductive effort and body lipid reserves may be more complex than previously thought.

Résumé : Un aménagement halieutique efficace nécessite une meilleure compréhension des mécanismes explicatifs de la variabilité du recrutement. Des études récentes laissent croire que la quantité et la qualité des gamètes produits par un poisson sont intimement liées à la disponibilité d'énergie excédentaire, généralement accumulée sous forme de lipides. Nous avons échantillonné des dorés (*Sander vitreus*) matures de sept populations provenant de divers sites d'un bout à l'autre du Canada afin de déterminer si les indices d'effort reproductif sont en relation positive avec les indices d'accumulation de nutriments chez les adultes, en particulier avec le contenu lipidique du corps. Il y a parmi les populations une forte variation dans les taux de croissance, les contenus lipidiques du corps et les caractéristiques reproductives. Les tendances à l'intérieur de chaque population sont très variables entre les indices d'effort reproductif et les caractéristiques corporelles des parents. La concentration de lipides dans le corps est plus souvent reliée à la concentration de lipides dans les gonades, mais pas dans toutes les populations. Dans l'ensemble des populations, il y a une corrélation positive entre la fécondité relative et le contenu lipidique des ovaires, ainsi qu'une corrélation négative entre la taille des oeufs et le contenu lipidique du corps entier; aucune tendance ne ressort chez les mâles. Nos résultats indiquent que les relations entre l'effort reproductif du doré et les réserves corporelles de lipides sont plus complexes qu'on ne le croyait.

[Traduit par la Rédaction]

Introduction

There is general agreement in fisheries science that recruitment is influenced by characteristics of the breeding population (Hilborn and Walters 1992). However, the nature of this relationship is still a key uncertainty in fisheries management. Recruitment is typically estimated from mature female biomass, a variable that integrates both the number and the size of adult females in the spawning stock, because it is an index of fecundity (Ricker 1954; Hilborn and Walters 1992; Myers 2001). In some species and populations, recruitment seems to be positively correlated with spawner biomass (Myers and Barrowman 1996; Chen and Holtby 2002), but in others, it does not (Mertz and Myers 1996; Marshall et al. 2003). To resolve this uncertainty, it is important to better understand the mechanisms driving variability in reproductive success within and among populations.

Though the quantity of gametes can play a key role in reproductive success, the quality of gametes may also be an important factor. The quality of gametes can be broadly defined as those traits that increase the fitness of the resultant

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offspring (Brooks et al. 1997). For example, egg size is often considered an index of quality because it reflects the amount of resources available for early growth and survival of the offspring (Roff 1992). Furthermore, both the quantity and quality of gametes may be related to parental traits other than biomass. Egg size is most often related to maternal body size and (or) maternal age (Bernardo 1996; Johnston and Leggett 2002); it may also be related to other maternal traits, though this has received less attention. The implication is that recruitment may depend as much on qualitative aspects of the spawning stock and its gametes as on spawning stock biomass and fecundity. Further research is required to determine how gamete quality is related to parental traits and how this may ultimately influence the stock–recruitment relationship.

Recent reviews have emphasized the importance of lipids in the development of the embryo and subsequent larval growth (Wiegand 1996; Rainuzzo et al. 1997; Tocher 2003); therefore, gonad lipid reserves may reflect gamete quality. Because fish allocate acquired energy to fulfill both current and future needs (Roff 1992; Crawford and Balon 1996; Adams 1999), the proportion of body lipids allocated to gamete production should be a function of the total lipids currently available and the individual's anticipated future requirements (Wiegand 1996). Variation in egg quality with respect to maternal traits (Bromage 1995; Brooks et al. 1997) and the role of lipids in gamete quality has led to questions about how the lipid status of the adult influences reproductive effort. In Atlantic cod (*Gadus morhua*), a positive correlation was found between fecundity and female liver lipid content (Marshall et al. 1999), and the absence of lipid-rich prey has been implicated as a contributor to population collapses (Rose and O'Driscoll 2002). There is also evidence from other iteroparous species (including walleye, *Sander vitreus*) suggesting that females may skip spawning events when their energy stores are too low (Henderson et al. 1996; Rideout et al. 2000, 2005). Despite these findings, little research has been directed at testing the relationships between the lipid stores of an individual and the quantity and quality of their gametes. Furthermore, previous research has focused solely on individual populations, making it difficult to assess the generality of such relationships.

Most research on the role of lipids in fish reproduction has centered on females, with far less research directed toward understanding the role that lipids may play in male reproductive success. Instead, quality of sperm is normally evaluated by traits such as motility, concentration, and fertilizing capacity (Billard et al. 1995) and is often correlated to parent condition (Rakitin et al. 1999; Casselman 2003; Trippel and Neil 2004), but not by lipid content. To date, consideration of male energy utilization during spawning has been dominated by the theory that energy is primarily allocated towards mating behaviours that influence male–male competition, mate selection, spawning, and parental care (Roff 1992; Crawford and Balon 1996), and little attention has focused on whether lipids influence gonadal development in males.

The goal of this research was to test the strength of relationships between reproductive effort and adult characteristics, particularly body lipid status, both within and among fish populations. We predicted that individuals with higher lipid levels in their bodies (i.e., more energy-rich individuals) would allocate more lipids to gamete production, and this would result in larger and more lipid-rich gonads in both sexes and higher fecundities and larger eggs in females. We tested these predictions by assessing whether variation in gonad and gamete traits were related to variation in a suite of adult traits, including lipid status, that were all believed to influence reproductive performance. This approach allowed us to assess the importance of lipid status to reproductive traits in relation to other adult traits, such as age, size, and body condition.

We addressed these predictions using the walleye, an iteroparous, broadcast-spawning fish native to central North American lakes and rivers. It is a primary target of recreational, commercial, and subsistence fisheries and among the most economically valuable species of all freshwater fishes in Canada. It is native over a broad geographical range, and stocks generally contain a range of ages and sizes of adults that spawn in the spring over a relatively short time period. Previous research has indicated that female walleye maturation depends on available lipid stores and that spawning events may be skipped by females if their energy stores are too low (Henderson et al. 1996). In addition, offspring quality as measured by egg size and hatching success has been shown to vary positively with maternal age and size (Johnston 1997; Johnston et al. 2007).

We examined the reproductive characteristics of male and female walleye both within and across a range of populations varying widely in adult characteristics, including reproductive effort and body lipid status. To achieve this, we selected populations across wide gradients of climate and exploitation. Walleye fecundity and egg size have been shown to decline with decreasing temperature or increasing latitude (Baccante and Colby 1996; Johnston and Leggett 2002); therefore, the role lipids play in gamete number and quality may also vary over the same gradient. Furthermore, life history traits in fishes, including gamete quantity and quality as well as energy availability, can rapidly respond to human exploitation (Craig et al. 1995; Trippel 1998).

Materials and methods

Population selection and field sampling

Mature walleye were sampled from seven populations across Canada (Fig. 1), covering a range of climates and exploitation histories (Table 1). We characterized climate by mean annual growing degree days above 5 °C from 1970 to 2000. Data were obtained from Environment Canada for the meteorological station situated closest to each lake. We categorized recent exploitation histories (low or high) based on the assessments of local fisheries managers. Populations designated as low exploitation (Trout Lake, Lac Beauchêne) were believed to be at high abundances relative to historic conditions at the time of sampling. However, populations designated as high exploitation were believed to range in relative abundances from collapsed and very low (Winefred Lake), to moderate (Lake Nipissing, Lake Ontario), to high (Lake Winnipeg, Lake of the Woods). Sampling was conducted during the spring spawning period from 2002 to 2004; dates of sampling varied from early April in the south to late May in the north. Populations were sampled immedi-

Fig. 1. Locations across Canada of the seven walleye (*Sander vitreus*) populations sampled for this study. Numbers correspond to the populations listed in Table 1.

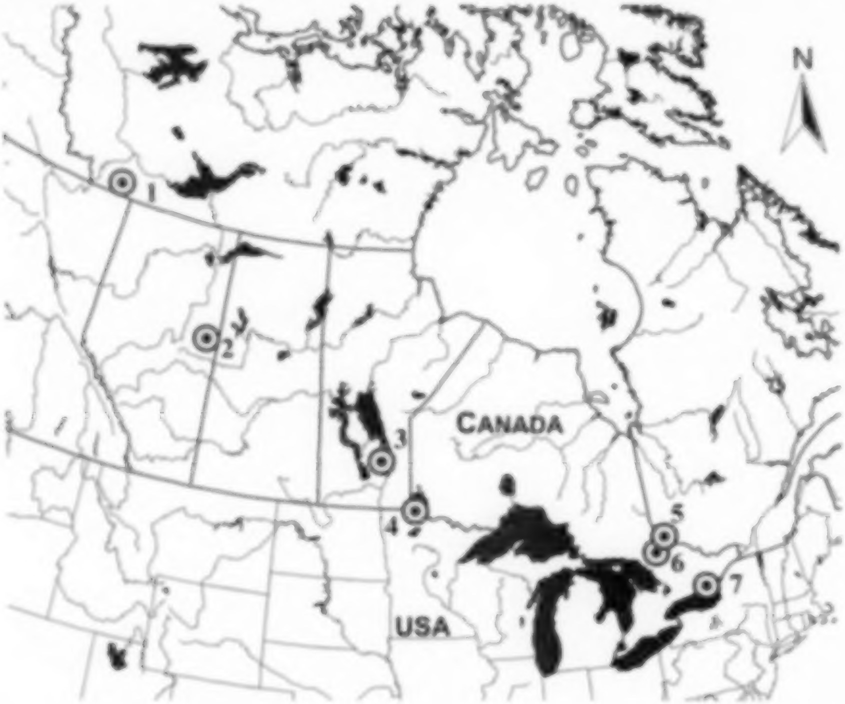


Table 1. Locations, sampling years, recent exploitation history, and climate characteristics for the seven lakes containing the walleye (*Sander vitreus*) populations sampled in this study.

Population	Years sampled	Latitude (°N)	Longitude (°W)	Exploitation	GDD > 5 °C
1. Trout Lake	2002, 2003	60°30′	121°30′	Low	1225
2. Winefred Lake	2004	55°20′	110°40′	High	1365
3. Lake Winnipeg	2002–2004	51°01′	96°53′	High	1551
4. Lake of the Woods	2004	49°09′	94°07′	High	1711
5. Lac Beauchêne	2002	46°30′	78°45′	Low	1642
6. Lake Nipissing	2002, 2003	46°12′	79°24′	High	1682
7. Lake Ontario	2002–2004	44°00′	76°40′	High	2145

Note: Populations are listed from north to south. GDD > 5 °C, growing degree days above 5 °C.

ately prior to or during the spawn, such that most individuals in the spawning runs had fully developed gonads. Fish were captured using dip nets, trap nets, or gill nets depending on local circumstances. Roughly equal numbers of mature, ripe males (i.e., semen free-flowing) and mature, prespawn females (i.e., eggs not free-flowing) were selected haphazardly, except with respect to body size. We deliberately attempted to obtain a wide size range of both sexes from each population. All individuals were killed by a blow to the head, packed on ice or frozen, then transported to the laboratory for further processing.

Fish processing and laboratory analyses

Each individual was weighed (total mass, ±10 g wet) and measured from the tip of the snout to the fork of the caudal fin (fork length (FL), ±1 mm). All tissue samples described below were kept in small plastic bags at –20 °C once removed from the carcass. For each male, testes were removed, weighed (±0.1 g wet), and frozen. For each female, ovaries were removed and weighed whole (±1 g wet), and then a subsample (~30 g) of ovary was removed from the midregion, weighed (±0.1 g wet), and frozen. For females that were frozen prior to processing, we removed and subsampled the ovaries in a frozen state to ensure that ova remained intact prior to freeze-drying (see below). The subsequent processing was similar for both sexes. The carcass was weighed without gonads (somatic mass, ±10 g wet), then the liver was removed, weighed (±0.1 g wet), and frozen. The carcass was weighed a final time following the removal of all remaining viscera posterior to the pericardial cavity (eviscerated mass, ±10 g wet). A subsample of skinless muscle (~30 g) was removed from alongside the first dorsal fin just above the lateral line, weighed (±0.1 g wet), and frozen. Sagittal otoliths were removed, rubbed clean, then placed into 5 mL plastic vials and allowed to air dry. Opercle bones were removed and frozen. The remaining carcass was then placed in a large plastic bag with the viscera (minus liver) and frozen at −20 °C.

All fish tissues underwent further processing prior to total lipid analyses. Carcasses with viscera were thawed, cut coarsely into pieces, and homogenized by passing three times through a commercial stainless steel meat grinder. A subsample (~25 g) of the homogenate was weighed (±0.1 g wet) in a glass vial and frozen at −20 °C. Ovary samples, testes, livers, muscle samples, and carcass homogenate subsamples were all freeze-dried for 7 days and reweighed (±0.1 g dry) to estimate moisture contents. Two subsamples of 30 freeze-dried ova were weighed (±0.01 mg) to estimate mean dry mass per ovum. Egg size was then estimated as mean wet mass per ovum using the mean dry mass and the corresponding moisture content. Fecundity was estimated as ovary wet mass divided by mean wet mass per ovum.

Total lipid contents of the freeze-dried tissues were determined gravimetrically (by weight) using a chloroform–methanol extraction procedure modified from earlier studies (Folch et al. 1957; Herbes and Allen 1983). All freeze-dried tissues were reduced to a coarse powder in a ball mill. An aliquot of the powdered tissue (~0.20 g) was weighed (±0.0001 g) into a 15 mL glass centrifuge tube. Five millitres of chloroform–methanol solvent (2:1 by volume) was added to the tissue, and the tube was sealed with a teflon-lined cap. After soaking overnight (>12 h), the mixture was centrifuged (10 min at 1000*g*) and the supernatant transferred to a second centrifuge tube (hereafter, the supernatant tube) by glass pipette. One millitre of chloroform–methanol solvent was rinsed through the pipette into the supernatant tube following transfer. The residue in the first centrifuge tube received an additional 3 mL of chloroform–methanol and was vortexed and centrifuged again. The resulting supernatant was added to the supernatant tube followed by another 1 mL of solvent for rinsing the pipette (total supernatant volume ~10 mL). The solvent and lipid mixture was washed by adding 2.5 mL of 0.88% KCl (0.88 g KCl in 100 mL distilled water) solution to the supernatant tube, agitating on a wrist-action shaker (15 min), and then centrifuged for 10 min at 1000*g*. After drawing off and discarding the upper aqueous layer, the lower solvent layer was transferred to a preweighed (±0.0001 g) aluminum pan by glass pipette, and the pipette was rinsed twice (1 mL solvent each) into the pan. Pans were placed in a fume hood at room temperature for ~1 h to allow the solvent to evaporate, transferred to a desiccator for ~1 h, then weighed (±0.0001 g) to determine lipid mass. Two extractions were performed for all samples, and a third was carried out if the coefficient of variation for the first two exceeded 10%.

Ages were primarily determined by counting annuli on sagittal otoliths. Otoliths were allowed to air dry and then set in epoxy. Transverse, thin sections (360 ± 30 µm) were cut through the nucleus using a Buehler® Isomet low-speed saw. These sections or acetate replicas of these sections were interpreted following standard procedures (Casselman 1987; Casselman and Gunn 1992). Where ages could not be determined from otoliths (<10 fish), annuli were read from opercle bones. Opercles were soaked in hot water to remove all flesh, allowed to air dry, then read under a dissecting scope using reflected light. When counting annuli, the outer edge of the otolith or opercle was always counted as a complete annulus, because individuals were collected at spawning time (i.e., near their birth dates). One of our sample populations (Lake Winnipeg) contains both normal and slow-growing (dwarf) morphotypes of walleye (W. Lysack, Manitoba Conservation, Box 20, 1495 St. James Street, Winnipeg, MB R3H 0W9, unpublished data). For the purposes of this study, we restricted our analyses to the normal form. Normal fish were separated from dwarf fish based on size-at-age criteria (Moles 2006).

Statistical analyses

Moisture and lipid concentrations of each fish were estimated for the gonad, soma (body minus gonads), liver, and muscle samples. Lipid concentrations were first estimated on a dry mass basis (100 × g lipid·g dry tissue^{-1}), then converted to a wet mass basis (100 × g lipid·g wet tissue^{-1}) using corresponding moisture contents. Whole-body moisture and lipid concentrations were reconstructed from masses and moisture and lipid concentrations of the component tissue samples. Body condition was estimated as the residual from $\log_e$ wet mass vs. $\log_e$ FL regressions (i.e., observed $\log_e$ mass minus predicted $\log_e$ mass) (Kaufman et al. 2007). Mass–length regressions and their residuals were calculated for each combination of sex and population.

Dependent variables representing gamete quantity and quality included relative fecundity (RF = number of eggs·female body mass (g)$^{-1}$), gonadosomatic index (GSI = 100 × gonad mass (g)·somatic mass (g)$^{-1}$), egg size (mg wet), gonad lipid concentration (percentage of wet mass), and the percentage of whole body lipid that was allocated to the gonad (100 × gonad lipid (g)·body lipid (g)$^{-1}$). Independent variables representing parental traits included age (years), total body mass (g wet), total body lipid content (percentage of wet mass), condition (residual $\log_e$ mass), hepatosomatic index (HSI = 100 × liver mass (g)·somatic mass (g)$^{-1}$), and liver lipid content (percentage of wet mass). Definitions and derivations of each variable are summarized in Table 2.

Relationships between reproductive traits and parental traits were examined at two spatial scales: among individuals within populations and among populations themselves. Data were pooled across years for populations sampled over multiple years. Statistical analyses were conducted using linear models (GLM procedure; SAS Institute Inc. 1999). For our within-population analyses, we regressed each reproductive trait against all parental traits to determine which contributed most to variation in gamete quantity and quality. Multiple regression models were fitted using a stepwise selection procedure (REG procedure; SAS Institute Inc. 1999). All tests of significance for variable retention were based on partial *F* statistics (using type III sums of squares). Thus, each independent variable remaining in the final model explained a significant amount of dependent variable variation after accounting for all other retained independent variables.

Among-population relationships between reproductive traits and whole-body lipid concentrations were analyzed by linear regression, either simple or quadratic. For these analyses, we calculated adjusted mean population traits using an analysis of covariance (ANCOVA) model with total body mass as the covariate (LSMEANS option, GLM procedure;

Table 2. Definitions of variables representing gamete quantity and quality and parental characteristics.

Variable	Description
Gamete quantity and quality	
GSI	Gonadosomatic index (100 × gonad wet mass·somatic wet mass^{-1})
RF	Relative fecundity (number of eggs·g of female total wet mass^{-1})
Egg size	Mean wet mass of an individual egg (mg)
Gonad lipid	Concentration of lipid in the gonad (% of wet mass)
Gonad lipid allocation	Percentage of body lipid in the gonad (100 × gonad lipid·body lipid^{-1})
Parental trait	
Age	Age (years)
Total mass	Total wet body mass (g)
Body condition	Residual from the population regression of $\log_e$ total mass vs. $\log_e$ fork length
HSI	Hepatosomatic index (100 × liver wet mass·somatic wet mass^{-1})
Body lipid	Concentration of lipid in the total body (% of wet mass)
Liver lipid	Concentration of lipid in the liver (% of wet mass)

Table 3. Summary statistics for mature adult walleye (*Sander vitreus*) sampled from seven populations (unadjusted means ± 1 SE).

Population	*n*	Age (years)	Fork length (mm)	Total mass (g)	GSI (%)	HSI (%)
1. Trout Lake						
Male	40	15.38±0.49	520.6±3.6	1523.2±28.6	1.87±0.07	1.78±0.05
Female	39	14.46±0.33	538.8±4.1	1783.8±37.4	10.99±0.34	1.98±0.05
2. Winefred Lake						
Male	41	14.34±0.89	539.3±10.8	1920.3±105.8	2.97±0.12	2.02±0.05
Female	37	18.97±0.53	632.5±5.2	3292.5±84.2	25.52±0.42	2.09±0.05
3. Lake Winnipeg						
Male	97	4.74±0.16	368.4±7.2	640.9±43.1	1.35±0.06	1.80±0.05
Female	61	6.95±0.29	503.7±7.4	1781.7±82.4	13.46±0.30	2.63±0.06
4. Lake of the Woods						
Male	16	9.88±0.68	459.3±10.1	1147.7±88.9	1.20±0.15	1.93±0.10
Female	35	9.86±0.44	553.8±10.8	2321.4±154.4	16.47±0.44	2.43±0.09
5. Lac Beauchêne						
Male	40	8.55±0.69	473.5±8.4	1189.2±64.5	2.50±0.11	2.08±0.05
Female	33	13.66±0.76	602.5±8.0	2492.0±89.2	18.57±0.57	1.78±0.04
6. Lake Nipissing						
Male	58	6.76±0.33	398.1±6.9	736.5±37.2	2.05±0.09	1.71±0.06
Female	38	8.32±0.39	517.9±11.2	1879.3±135.3	17.40±0.34	2.33±0.08
7. Lake Ontario						
Male	71	9.18±0.57	544.7±10.1	2110.4±109.9	3.38±0.19	2.47±0.07
Female	41	9.71±0.67	628.7±12.5	3692.8±234.4	28.59±1.05	3.86±0.15

Note: Populations are listed from north to south. GSI, gonadosomatic index; HSI, hepatosomatic index.

SAS Institute Inc. 1999). Means were adjusted for each sex to the among-population mean total body mass: 1200 g for males and 2500 g for females.

Results

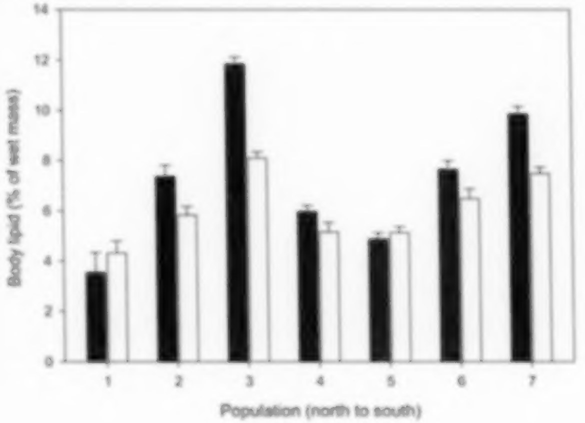
Adult characteristics

A total of 648 mature walleye were sampled for this study. We obtained ≥30 adults of each sex from each population, with the exception of males from Lake of the Woods (Table 3). Mean ages and sizes of sampled fish varied considerably among the seven populations (Table 3). Females ranged in FL and age from 403 to 760 mm and from 4 to 24 years, respectively. Males ranged in FL and age from 263 to 685 mm and from 2 to 22 years, respectively. Growth rates (length at age) generally declined from south to north and were lower in lightly exploited populations (Kaufman et al. 2007). Whole-body lipid concentrations varied from 1.6% to 15.8% in mature females and from 0.8% to 12.9% in mature males. Mean body lipid concentrations of females were higher than those of males, except in the two lightly exploited populations (Fig. 2). In general, populations characterized as lightly exploited tended to have lower lipid levels for both sexes, while more heavily exploited populations had higher lipid levels (Fig. 2). GSI values varied from 4.6% to 44.8% in females and from 0.3% to 9.4% in males. Female GSI generally increased from north to south, with the exception of the heavily exploited and collapsed population of Winefred Lake, which had higher GSI than expected.

Covariation of reproductive traits and adult traits: multiple regression analyses within populations

We tested if reproductive traits covaried with adult body lipid content while also accounting for associations with

Fig. 2. Mean whole-body lipid concentrations of mature, prespawn males (open bars) and females (solid bars) from seven walleye (*Sander vitreus*) populations. Numbers correspond to the populations listed in Table 1. Bars indicate the mean for the population + SE. Means are standardized to a common total body mass of 1200 g for males and 2500 g for females.



other potentially important parental characteristics, such as age, body size (total mass), body condition, liver mass, and liver lipid concentration.

Body mass or age accounted for significant variation in GSI for females in five of seven populations (Table 4) and the effect was consistently positive. Additional variation in female GSI was accounted for by HSI in Winefred Lake (positive effect) and by liver lipid content in Lakes Winnipeg and Ontario (negative effect). Body lipid was not retained in the analysis of any female population. For males, GSI was more consistently related to total body mass and to indices of body condition (Table 4). Male GSI was positively related to body lipid concentration in two populations.

RF was not significantly related to any of the maternal traits in any of the populations examined, with the exception of positive relationships with body condition (Lake Winnipeg) and HSI (Lake of the Woods) (Table 5). Egg size showed stronger relationships with maternal traits, but no single trait consistently accounted for significant variation. Egg size was positively related to maternal age or size in two populations, negatively related to HSI or liver lipid concentration in four populations, and positively related to body lipid content in two populations (Table 5).

Relationships between gonad lipid concentration and the parental traits were generally stronger than observed for RF and egg size, but were still quite variable among populations (Table 6). Gonad lipid concentration was most consistently related to HSI in females (four of seven populations) and to body lipid concentration in males (three of seven populations) (Table 6). Parental age or size had a weak negative effect on gonad lipid concentration in a few cases (Table 6).

The percentage of total body lipids allocated to the gonads showed a strong negative relationship with body lipid concentration in females of all populations (Table 7). Smaller amounts of the remaining variation were accounted for by other indices of age, body condition, and HSI in some populations. For males, gonad lipid allocation was negatively related to body lipid concentration in five of seven populations, but was also positively related to body mass and (or) HSI in six of seven populations (Table 7).

Covariation of reproductive traits and body lipid: variation among populations

Mean GSI of females increased with mean body lipid concentration across the seven populations, though the population with highest body lipid concentration (Lake Winnipeg, population #3) deviated from this trend (Fig. 3*a*), making the relationship nonsignificant (correlation analysis, $n = 7$, $r = 0.40$, $P = 0.37$). No clear trend was evident for males (Fig. 3*b*, correlation analysis, $n = 7$, $r = 0.13$, $P = 0.78$). For females, mean RF showed a positive trend, and mean egg size showed a negative trend with respect to mean body lipid concentration across the seven populations (Figs. 4 and 5), though neither of these trends were statistically significant (correlation analysis, $n = 7$; RF: $r = 0.66$; egg size: $r = -0.67$; P values > 0.10). Across the range of observed body lipid concentrations, RF was generally lower in the more northerly populations (Fig. 4).

The relationship between mean gonad lipid concentration and mean body lipid concentration was positive for females (correlation analysis, $n = 7$, $r = 0.89$, $P = 0.007$) and nonexistent for males (correlation analysis, $n = 7$, $r = 0.22$, $P = 0.64$) across the seven populations (Fig. 6). Lake Ontario males appeared to deviate strongly from the observations for males in other populations (Fig. 6, population #7). The proportion of whole-body lipid present in the gonads generally declined with increasing mean body lipid concentration in both sexes (Fig. 7), although the relationship was stronger in females (correlation analysis, $n = 7$, $r = -0.72$, $P = 0.067$) compared with males (correlation analysis, $n = 7$, $r = -0.46$, $P = 0.30$). These trends did not appear to be related to the climate or exploitation history experienced by the populations.

Discussion

The primary objective of this research was to examine the relationships between reproductive effort and adult traits and examine the generality of these relationships across populations that varied widely in these respects. We set out to determine if walleye reproductive effort was limited by adult quality, particularly as reflected by body lipid reserves. We predicted that individuals with higher lipid levels in their bodies would allocate more to gamete production and that this would result in larger and more lipid-rich gonads in both sexes and higher fecundities and larger eggs in females. Our approach differed from earlier studies in that we examined multiple populations varying widely in body lipid content and ecological context. Although seven populations afford relatively low statistical power for detecting significance in among-population trends, by examining relationships at two scales (among and within populations) and with respect to multiple parental traits, we have been able to test the generality of any relationships. Our results clearly indicate that in walleye the relationships among many reproductive and adult traits vary considerably among populations, that lipid may not be as limiting to reproductive effort as was previ-

Table 4. Results of stepwise multiple regression models of gonadosomatic index (GSI) against six adult characteristics performed separately on mature, prespawn male and female walleye (*Sander vitreus*) from seven lake populations.

	Adult characteristics											
	Age (years)		Total mass (g wet)		Body condition (residual log mass)		HSI (%)		Body lipid (% of wet mass)		Liver lipid (% of wet mass)	
Population	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2
Females												
1. Trout Lake												
2. Winefred Lake	+	0.11					+	0.14				
3. Lake Winnipeg	+	0.22									–	0.08
4. Lake of the Woods			+	0.14								
5. Lac Beauchêne					+	0.27						
6. Lake Nipissing			+	0.13								
7. Lake Ontario			+	0.24							–	0.17
Males												
1. Trout Lake									+	0.34		
2. Winefred Lake			+	0.42								
3. Lake Winnipeg	+	0.26					+	0.06	+	0.05		
4. Lake of the Woods					+	0.50						
5. Lac Beauchêne	–	0.12	+	0.52			+	0.04				
6. Lake Nipissing			+	0.09			+	0.08				
7. Lake Ontario			+	0.26								

Note: Effect indicates regression coefficient (positive or negative), and partial R^2 indicates the proportion of variance explained in the final model. Effects and partial R^2 values are listed only for adult characteristics that explained significant variation (partial F, $P < 0.05$) in GSI and were therefore retained in the final model. HSI, hepatosomatic index.

Table 5. Results of stepwise multiple regression of relative fecundity and egg size against six adult characteristics for mature, prespawn female walleye (*Sander vitreus*) from seven lake populations.

	Adult characteristics											
	Age (years)		Total mass (g wet)		Body condition (residual log mass)		HSI (%)		Body lipid (% of wet mass)		Liver lipid (% of wet mass)	
Population	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2
Relative fecundity (egg·g^{-1})												
1. Trout Lake												
2. Winefred Lake												
3. Lake Winnipeg					+	0.09						
4. Lake of the Woods							+	0.30				
5. Lac Beauchêne												
6. Lake Nipissing												
7. Lake Ontario												
Egg size (mg wet)												
1. Trout Lake												
2. Winefred Lake												
3. Lake Winnipeg	+	0.17									–	0.11
4. Lake of the Woods							–	0.26	+	0.09		
5. Lac Beauchêne									+	0.19		
6. Lake Nipissing							–	0.14				
7. Lake Ontario			+	0.10							–	0.10

Note: Effect indicates regression coefficient (positive or negative), and partial R^2 indicates the proportion of variance explained in the final model. Effects and partial R^2 values are listed only for adult characteristics that explained significant variation (partial F, $P < 0.05$) in the dependent variable and were therefore retained in the final model. HSI, hepatosomatic index.

Table 6. Results of stepwise multiple regression of gonad lipid concentration (% of wet mass) against six adult characteristics for mature, prespawn walleye (*Sander vitreus*) from seven lake populations.

	Adult characteristics											
	Age (years)		Total mass (g wet)		Body condition (residual log mass)		HSI (%)		Body lipid (% of wet mass)		Liver lipid (% of wet mass)	
Population	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2
Females												
1. Trout Lake												
2. Winefred Lake												
3. Lake Winnipeg			–	0.12			+	0.20				
4. Lake of the Woods							+	0.47				
5. Lac Beauchêne									+	0.48		
6. Lake Nipissing							+	0.15				
7. Lake Ontario	–	0.10					+	0.37				
Males												
1. Trout Lake									+	0.19		
2. Winefred Lake									+	0.16		
3. Lake Winnipeg												
4. Lake of the Woods												
5. Lac Beauchêne												
6. Lake Nipissing									+	0.11		
7. Lake Ontario	–	0.14										

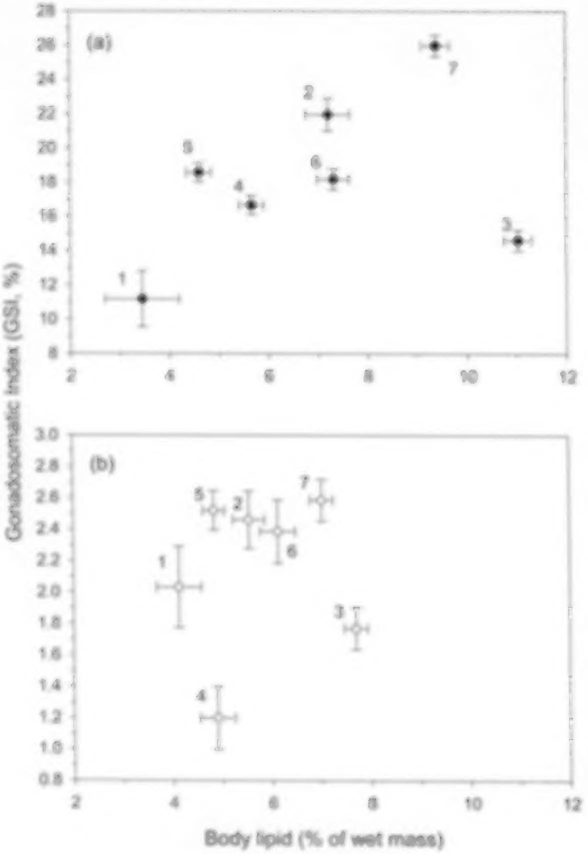
Note: Effect indicates regression coefficient (positive or negative), and partial R^2 indicates the proportion of variance explained in the final model. Effects and partial R^2 values are listed only for adult characteristics that explained significant variation (partial F, $P < 0.05$) in gonad lipid and were therefore retained in the final model. HSI, hepatosomatic index.

Table 7. Results of stepwise multiple regression of gonad lipid allocation (% of body lipid in gonad) against six adult characteristics for mature, prespawn walleye (*Sander vitreus*) from seven lake populations.

	Adult characteristics											
	Age (years)		Total mass (g wet)		Body condition (residual log mass)		HSI (%)		Body lipid (% of wet mass)		Liver lipid (% of wet mass)	
Population	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2	Effect	Partial R^2
Females												
1. Trout Lake									–	0.38		
2. Winefred Lake									–	0.56		
3. Lake Winnipeg	+	0.03							–	0.77		
4. Lake of the Woods	+	0.04							–	0.71		
5. Lac Beauchêne					+	0.10			–	0.52		
6. Lake Nipissing	+	0.04							–	0.83		
7. Lake Ontario							+	0.05	–	0.54		
Males												
1. Trout Lake									–	0.31		
2. Winefred Lake			+	0.25					–	0.07		
3. Lake Winnipeg			+	0.16								
4. Lake of the Woods							+	0.34				
5. Lac Beauchêne			+	0.32					–	0.17		
6. Lake Nipissing			+	0.09			+	0.07	–	0.09		
7. Lake Ontario	–	0.07	+	0.10			+	0.04	–	0.23		

Note: Effect indicates regression coefficient (positive or negative), and partial R^2 indicates the proportion of variance explained in the final model. Effects and partial R^2 values are listed only for adult characteristics that explained significant variation (partial F, $P < 0.05$) in allocation and were therefore retained in the final model. HSI, hepatosomatic index.

Fig. 3. Among-population relationships between gonadosomatic index (GSI) and body lipid concentration for mature, prespawn female (*a*) and male (*b*) walleye (*Sander vitreus*) from seven populations. Numbers correspond to the populations listed in Table 1. Symbols indicate population means adjusted to a common total body mass (2500 g for females, 1200 g for males) ± SE. Note that *y*-axis scales differ between sexes.



ously assumed, and that adult lipid status may influence reproductive effort differently in the two sexes.

We used GSI as our index of total reproductive effort and found that relationships between GSI and body lipid status varied with the scale of analysis, indicating little consistent evidence of a strong causal relationship. For females, the relationship was weakly positive across populations; no clear trend was evident for males. When compared with other parental traits, body lipid content was not a strong predictor of reproductive effort, particularly in females where body mass was the most consistent predictor of GSI. For males, the weak relationship between GSI and body lipid reserves may be taken as evidence supporting the theory that energy is allocated to mating behaviours (Crawford and Balon 1996; Roff 2002); however, body lipid was positively related to GSI in three populations, suggesting that gonadal development may be important as well.

The strong relationship between body size and gonad GSI was expected, since larger individuals can physically accommodate larger gonads in their bodies. However, we expected that the remaining variation would be positively related to body lipid concentration if lipids were a limiting factor in gonad formation. The lack of a strong relationship could mean that the terminal size of the gonad at spawning is not dependent on available lipids or that it is dependent on the adult lipid status at some earlier date in the annual maturation cycle. Regarding this latter possibility, research on Lake Erie adult walleye has shown that while soma and gonad lipid concentrations covary inversely over the annual cycle, whole-body lipid concentrations remain fairly stable (Henderson et al. 1996). Thus, whole-body lipid concentrations at spawning may be representative of the whole season. It is unknown if seasonal variation in whole-body lipid concentrations was similar in our study populations. Gonad

Fig. 4. Among-population relationship between relative fecundity and body lipid for mature, prespawn female walleye (*Sander vitreus*) from seven populations. Numbers correspond to the populations listed in Table 1. Symbols indicate population means adjusted to a common total body mass of 2500 g ± SE.

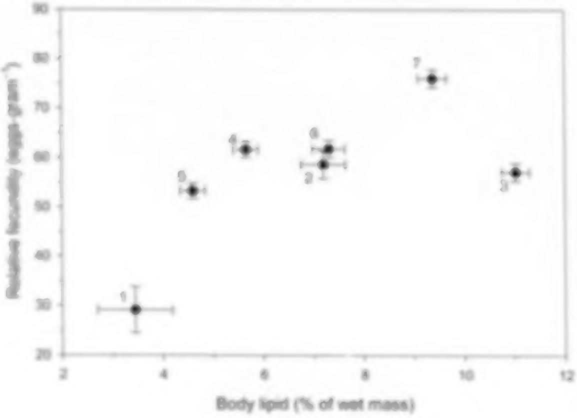


Fig. 5. Among-population relationship between egg size and body lipid for mature, prespawn female walleye (*Sander vitreus*) from seven populations. Numbers correspond to the populations listed in Table 1. Symbols indicate population means standardized to a common total body mass of 2500 g ± SE.

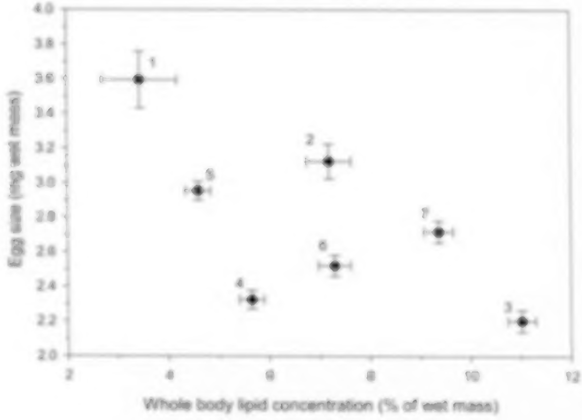


Fig. 6. Among-population relationship between gonad lipid and body lipid for mature, prespawn female (*a*) and male (*b*) walleye (*Sander vitreus*) from seven lake populations listed in Table 1. Symbols indicate population means standardized to a common total body mass (1200 g males, 2500 g females) ± SE. Note that *y*-axis scales differ between sexes.

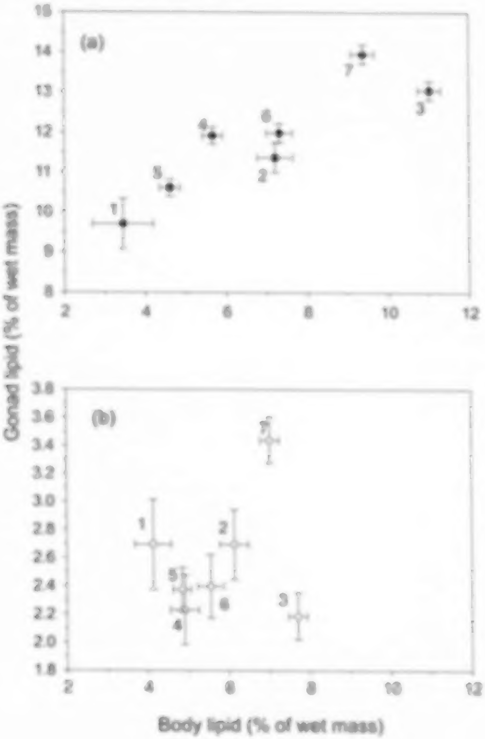
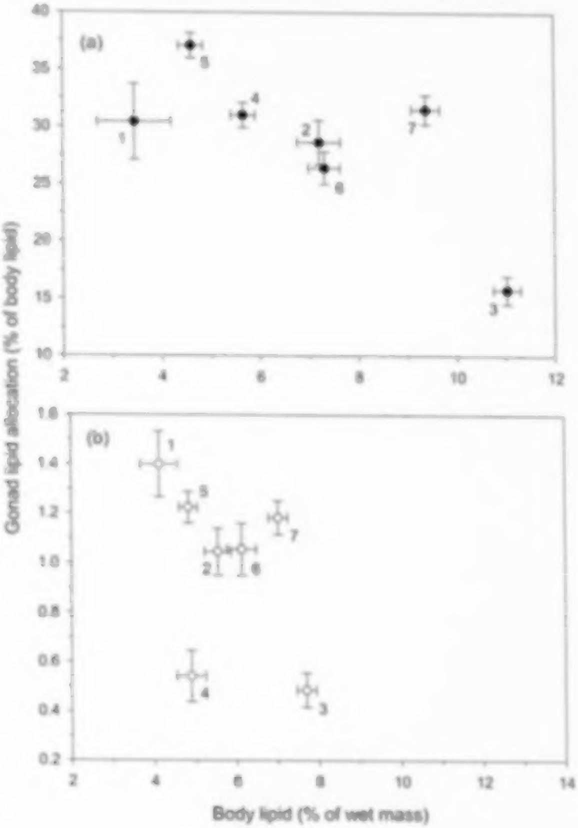


Fig. 7. Among-population relationship between gonad lipid allocation and body lipid in mature, prespawn female (*a*) and male (*b*) walleye (*Sander vitreus*) from the seven lake populations listed in Table 1. Symbols indicate population means standardized to a common total body mass (1200 g males, 2500 g females) ± 1 SE. Note that *y*-axis scales differ between sexes.



size has been shown to be related to other indices of body nutrient reserves, such as condition, in some species (Yoneda and Wright 2005).

We subdivided female gonadal investment into two components, RF and egg size, for further analyses. There was no strong or consistent relationship between RF and any maternal traits in most populations examined. With a few exceptions, the same was true for egg size. However, across populations, mean fecundity increased and mean egg size decreased with respect to mean body lipid concentrations. RF was generally lower in the more northerly walleye populations, a trend consistent with earlier research for this species (Baccante and Colby 1996).

Strong relationships between fecundity and body size are common in a wide variety of taxa (Roff 1992), and in fishes, the relationship is usually positive (Wootton 1979). The effects of other maternal traits on fecundity appear to be more variable, and their significance often depends on which measure of maternal size is included as a covariate. For example, fecundity has been linked with female condition in some fishes when it is first adjusted for body length but not when it is adjusted for body mass (Koops et al. 2004). Previous research has suggested that fecundity may be highly dependent on the amount of lipid available for reproduction (Marshall et al. 1999, 2000; Thorpe 2004), whereas other studies, including this one, have found that lipid stores may be a poor proxy in predicting fecundity in a population (De Oliveira et al. 2006; Skjæraasen et al. 2006). As already discussed, a weak relationship could mean that fecundity is either not limited by available lipids or that it is dependent on the adult lipid status at some earlier point in the ovarian cycle. For example, fecundity in Atlantic cod appears to be more closely related to maternal energy stores several months prior to spawning than at the time of spawning (Skjæraasen et al. 2006).

Variability in fecundity relative to egg quality may depend on the timing of nutrient availability to the mother during the ovarian cycle. In walleye, vitellogenesis begins in the previous autumn (Malison et al. 1994), and oocyte recruitment must occur prior to this. Thus, maximum potential fecundity would be established by late summer, if not earlier, and may reflect the maternal physiological state at that time. Following oocyte recruitment, the female could decrease (through atresia) but not increase fecundity. If the nutrients available for reproduction decrease from before to after oocyte recruitment, the female could compensate by reducing egg number or size or by halting vitellogenesis altogether. In contrast, if the available nutrients were to increase between the two periods, the female could only increase the provisioning per egg, not the number of eggs. If this is the case, we predict that egg quality rather than egg quantity will be more strongly dependent on maternal lipid status at the end of the ovarian cycle.

Egg size is the primary determinant of offspring size at hatch and therefore has a strong effect on early growth and survival in fishes (Miller et al. 1988). Whereas fecundity influences only maternal fitness, egg size influences both maternal and offspring fitness (Bernardo 1996), and females may sacrifice egg size at the expense of increased fecundity (Einum and Fleming 2000). We predicted that egg size would be positively related to maternal age or size and indices of the female's nutrient reserves. Where such relationships were significant, they were indeed positive. However, egg size was not consistently related to any female trait that we examined. The relationships between egg size and maternal size or age in walleye appear to be highly variable among populations, consistent with other studies (Johnston and Leggett 2002). There is evidence that egg size is positively related to maternal condition in some fishes (Chambers and Waiwood 1996; Marteinsdottir and Steinarsson 1998; Trippel and Neil 2004), although we observed no such relationship in these walleye populations.

Another strategy for adults with surplus energy to increase their gamete quality may be to produce gonads with a higher lipid concentration, providing offspring with greater energy reserves. The relationship between gonad and body lipid concentrations has not been extensively studied, although positive relationships have been reported for females of some fish species (Bunnell et al. 2005). For females, producing eggs of higher lipid content may yield offspring with more rapid early growth (Brown and Taylor 1992). For males, a more lipid-rich gonad may allow production of more sperm or the production of sperm with greater energy and faster swimming speeds. There is some evidence that sperm adenosine triphosphate (ATP) content is related to male condition (Casselman 2003). Our analyses indicated that the relationship between high body lipid levels and lipid-rich gonads varied between the sexes. For males, the among-population relationship appeared negative, while among female populations the relationship between gonad lipid concentration and body lipid concentration was positive. When examined in relation to a suite of other adult traits, effects of body lipid concentration on gonad lipid concentration were statistically significant in one population for females and three populations for males. For females, indices of liver size, such as HSI, appeared to be stronger predictors of gonad lipid concentration.

We also predicted that individuals with elevated body lipid concentrations would commit a higher proportion of their lipid reserves to gonad formation. Our results did not support this prediction; instead, lipid allocation to the gonad was negatively related to body lipid concentration in all female and most male populations. This could be explained if there was an upper limit to gonadal investment such that individuals could not exceed the limit regardless of their lipid stores. An upper limit with respect to lipids may be the result if gonadal development were limited by another component required in the process. If an upper limit exists, then the amount of lipids committed to gonads would be relatively smaller in a lipid-rich individual compared with a lipid-poor individual.

Life history theory predicts that, all else being equal, selection should favor individuals with greater energy to increase either the number or quality of their offspring (Stearns 1992). Thus, the ability to alter reproductive effort in response to fluctuations in resource availability might evolve in many populations. Our results suggest that the relationship between energy availability, as reflected in body or liver lipid content, and gonadal investment in walleye is not so simple and may have to take into account various constraints. For example, physiological constraints may limit the evolution of flexible reproductive efforts if the temporal scale of any physiological allocation response is longer than the scale of resource fluctuations. This could explain why many individuals with seemingly high body lipid reserves make relatively small investments to their gonads. This may also explain why relationships between some reproductive traits (e.g., gonad size) and adult lipid status appear stronger among populations than within populations, because trends at the population level may reflect longer-term variation in environmental conditions that can be tracked by a flexible physiological allocation response.

Promising areas for future research are to examine various alternative hypotheses arising from this work. One hypothesis, for example, is that gonad development becomes limited by adult lipid reserves only below some critical threshold and is limited by other nutritional factors (availability of protein, minerals, etc.) above that threshold. This may be worth investigating in the Lake Winnipeg walleye population, where gonadal investment appears to be relatively low despite very high adult body lipid content. A second hypothesis is that life history decisions about annual gonadal investment may be more strongly regulated by recent past (i.e., prior 1–2 years) growth history than by current nutrient reserves. Because growth rate and mortality in fishes are often inversely related (Craig 1985), such a mechanism could allow fishes to adjust their reproductive effort in relation to their perceived lifespan rather than adjusting it to some sliding window of current or recent resource levels.

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Body condition influences sperm energetics in lake whitefish (*Coregonus clupeaformis*)

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Abstract: Theoretical models predict that individual males will increase their investment in ejaculates when there is a risk of sperm competition. Because the production of ejaculates is assumed to be energetically costly, only those males in good physical condition should be capable of producing ejaculates of high quality. We studied ejaculate investment (relative testis size, controlling for body size) as well as the size, behaviour, and energetics of spermatozoa in lake whitefish (*Coregonus clupeaformis*), a species in which males provide nothing but sperm to females during reproduction. Ejaculate investment was condition dependent, with males in better body condition having relatively larger testes. Sperm adenosine triphosphate (ATP) levels were unaffected by male condition alone, but increased with testis size when controlling statistically for both male size or body condition. Thus, males investing in relatively larger testes produced spermatozoa with higher energetic capacity. We also discovered testis asymmetry in this species, a phenomenon not previously reported in fishes, though widespread in other taxa. The mass of the (larger) left testis was a better predictor of sperm ATP stores than the mass of the (smaller) right testis (controlling for body size), suggesting that testis size asymmetry might be related to the production of high-quality sperm.

Résumé : Les modèles théoriques prédisent que les mâles individuels soumis à un risque de compétition spermatique vont augmenter leur investissement dans leur éjaculat. Comme on présume que la production d'éjaculat a un coût énergétique élevé, seuls les mâles en bonne condition physique devraient être capables de produire des éjaculats de grande qualité. Nous étudions l'investissement dans l'éjaculat (taille relative des testicules, compte tenu de la taille corporelle), ainsi que la taille, le comportement et les relations énergétiques des spermatozoïdes chez le grand corégone (*Coregonus clupeaformis*), une espèce chez laquelle le mâle ne fournit que le sperme aux femelles durant la reproduction. L'investissement dans l'éjaculat est fonction de la condition, car les mâles en meilleure condition corporelle possèdent des testicules relativement plus gros. Les concentrations d'adénosine triphosphate (ATP) dans les spermatozoïdes ne sont pas affectées par la condition seule, mais elles augmentent en fonction de la taille des testicules, une fois qu'on a tenu compte statistiquement de la taille du corps et aussi de la condition corporelle des mâles. Ainsi, les mâles qui investissent dans des testicules relativement plus gros produisent des spermatozoïdes de capacité énergétique supérieure. Nous avons aussi découvert une asymétrie des testicules chez cette espèce, un phénomène non encore signalé chez les poissons, bien que courant dans d'autres taxons. La masse du testicule gauche (plus gros) s'avère être une meilleure variable explicative des réserves d'ATP des spermatozoïdes que la masse du testicule droit (plus petit), une fois qu'on a fait les corrections pour tenir compte de la taille corporelle; cela laisse croire que l'asymétrie de la taille des testicules peut être reliée à la production de spermatozoïdes de qualité supérieure.

[Traduit par la Rédaction]

Introduction

Sperm competition is widespread in nature and occurs when the sperm of two or more males compete to fertilize a female's ova (Parker 1970). It is a powerful influence on selection, responsible for variation in male behaviour, anatomy, and physiology (Birkhead and Møller 1998). Sperm are produced in the testes, and because the size of the testes reflects ejaculate investment (Scharer et al. 2004), the testes are predicted to be larger in species with more intense sperm competition. Comparative studies across numerous vertebrate taxa have detected general support for this prediction (e.g., Mammals: Harcourt et al. 1981; Fish: Stockley et al. 1997; Amphibians: Byrne et al. 2002).

Within species, ejaculate quality (e.g., sperm density, motility, swimming speed, and adenosine triphosphate (ATP) stores) also varies among individuals (reviewed in Snook 2005) and can result in differential fertilization success (e.g., Casselman et al. 2006). Numerous factors have been shown to influence ejaculate quality, including age (e.g., Evans and

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Geffen 1998), body size (Skinner and Watt 2007), mating tactic (e.g., Uglem et al. 2001; Vladic and Järvi 2001), and social status (e.g., Rudolfsen et al. 2006).

A fundamental assumption underlying much of sexual selection theory is that traits associated with male–male competition and female mate choice should be costly to produce (Andersson 1994). Production of ejaculates can be energetically demanding (Olsson and Madsen 1998), and thus only males in good body condition are predicted to produce high-quality ejaculates. In fishes, males in better body condition have been shown to have higher fertilization success (e.g., Rakitin et al. 1999), and the eggs they fertilize have higher survival rates (Wedekind and Müller 2004), but relations between ejaculate investment (testis size and sperm parameters) and body condition factors have been rarely considered (e.g., Casselman and Montgomerie 2004; Jonsson and Jonsson 2006).

In the current study, we examined intraspecific variation in ejaculate investment in male lake whitefish, *Coregonus clupeaformis*. The mating system of lake whitefish is not well understood, but they are considered to be group spawners (Wedekind et al. 2001), suggesting that sperm competition is likely to be an important, selective force in this species. We examined relations among ejaculate investment (testis size); ejaculate quality (swimming speed, percent motility, density, and ATP stores of sperm); and the age, size, and body condition of individual male lake whitefish to test the predictions that (*i*) ejaculate investment is dependent upon body condition — males in good condition should have larger testes and higher-quality ejaculates than males in poor condition; and (*ii*) younger and (or) smaller males have greater relative investment in testes and ejaculate quality than larger, older males to compensate for their presumed disfavoured role during spawning as a result of dominance by larger males.

Like males of many other vertebrates (Birkhead et al. 1998), male lake whitefish have asymmetrical testes (see below), with the left testis being larger than the right. Reasons for testis size asymmetry are generally unknown, though one suggestion has been that the smaller testis provides insurance in case of damage or disease impairing sperm production in the larger testis. If the larger testis becomes impaired, then the smaller testis may increase in size to compensate, thereby reducing the degree of testis asymmetry (Møller 1994; Birkhead et al. 1998). Thus, this directional asymmetry may be positively related to measures of male quality, with high-quality males having more asymmetrical testis (Møller 1994). To test this hypothesis, we examined the relative importance of right and left testis size as predictors of sperm energetics.

Materials and methods

Sampling and handling

Adult male lake whitefish were captured in 2002 during fall spawning in the Bay of Quinte, Lake Ontario, Canada. Twenty-five males were captured in traps, transported to shore, and held in aerated holding tanks filled with lake water at 7 °C until they were stripped of milt (within 8 h of being brought to shore). Twenty-four additional males were stripped of milt immediately following removal from the trap so that we could preserve additional sperm samples for morphological analysis; no measures of sperm motility or ATP content were performed on these 24 males. Milt was collected by applying pressure to the male's abdomen and taking up the extruded milt into 1 mL syringes. Samples for motility and ATP content were used immediately; all other samples were stored on ice for up to 4 h before processing. Milt contaminated with either urine or feces was discarded.

Following milt collection, all fish were killed and their fork length (FL ± 1 mm) and body mass (±1 g) recorded. Left and right testes were removed and weighed (±1 g). Male age for 47 individuals was determined from sagittal otoliths, following Casselman and Montgomerie (2004).

Ejaculate quality

See Burness et al. (2004) for details of our methods for measuring sperm motility. We first used 750 μL of Cortland's solution (250 $\mathrm{mmol \cdot L^{-1}}$ NaCl, 10 $\mathrm{mmol \cdot L^{-1}}$ KCl, 3 $\mathrm{mmol \cdot L^{-1}}$ $CaCl_2$, 24 $\mathrm{mmol \cdot L^{-1}}$ $NaHCO_3$, at pH 7.91, ~500 mosmol) to dilute 5 μL of the milt without activating the sperm. We then placed a drop of this solution into a hemocytometer chamber and initiated motility by flooding the sample with lake water at 7 °C. We recorded sperm motility on videotape using a high-resolution CCD camera mounted on a negative phase contrast microscope with the microscope stage maintained at ambient lake temperature (7–10 °C).

We analyzed videotapes using a CEROS (v. 12) sperm analysis system (Hamilton Thorne Research, Beverly, Massachusetts, USA). For each male, we calculated sperm swimming speed (VAP; average smoothed path velocity) for up to 35 spermatozoa per field of view, for each of seven time intervals from 0.5 to 90 s after activation, using criteria for selection of individual sperm reported in Burness et al. (2004). Here, we report only VAP (Casselman and Montgomerie 2004) at 10 s after activation, because the majority of fertilizations have been reported to occur within the first few seconds following ejaculation in externally fertilizing fishes (Vladic and Järvi 1997; Hoysak and Liley 2001). We use median VAP in all analyses to minimize the influence of both outliers and skewed distributions of swimming speeds (Casselman et al. 2006). At 10 s after activation, we measured VAP for a mean of 23 sperm per field of view (±1.3 standard error (SE), range 9–33 sperm, $n = 24$ fish).

To calculate the percentage of sperm that were motile within an ejaculate, we placed a piece of acetate over the computer monitor and marked each spermatozoon as either swimming or immotile at both 10 s and 60 s after activation. We performed this analysis twice for each of 10 males at 10 s after activation and found that the estimates were highly repeatable (repeatability = 0.95, $P < 0.001$).

To preserve sperm for morphological analysis, we diluted milt 151-fold in fixative (2.5% glutaraldehyde in 0.1 $\mathrm{mol \cdot L^{-1}}$ sodium cacodylate buffer, pH 7.0), then spread the solution evenly across a microscope slide and allowed it to air-dry. Sperm tail length was measured from digitized images of sperm from these slides (see Burness et al. 2004). Sperm concentration was measured by counting the number of sperm in 10 haphazardly chosen hemocytometer cells (see Leach and Montgomerie 2000).

To measure sperm ATP content, 20 μL of fresh milt, from each of the males for which we measured sperm motility,

Table 1. Descriptive statistics for morphological and ejaculate traits of male lake whitefish (*Coregonus clupeaformis*).

Trait	Mean±SE	95% CL	Range	*n*
Morphological				
Age (years)	8.8±0.3	8.2–9.3	5–12	45
Fork length (mm)	452.9±5.0	442.9–463.0	360–538	47
Body mass (g)	1001.9±38.1	925.1–1078.6	472–1712	47
Fulton's *K*	1.05±0.01	1.03–1.08	0.89–1.25	47
Left testis mass (g)	8.38±0.56	7.26–9.51	3–19	47
Right testis mass (g)	6.74±0.46	5.81–7.68	3–19	47
Ejaculate				
Median sperm length (μm)	38.4±0.4	37.6–39.2	30.4–44.7	47
Sperm density (no. × 10^6·(μL milt)$^{-1}$)	6.25±0.21	5.83–6.67	3.26–9.85	47
Median VAP (μm·s^{-1}) at 10 s after activation	112.5±2.0	108.5–116.8	93.2–129.1	23
Percent motility at 10 s after activation	60.6±2.8	54.8–66.4	34–79	23
Percent motility at 60 s after activation	32.1±3.6	24.7–439.5	5–68	24
ATP levels (pmol·(million sperm)$^{-1}$)	139.0±9.1	120.1–157.9	51.5–236.5	23

Note: Two outliers were removed from all analyses and one additional outlier was removed from the ATP analysis. SE, standard error; CL, confidence limit; VAP, average smoothed path velocity (sperm swimming speed).

was frozen on dry ice in the field and stored at –80 °C until ATP content was measured (see Burness et al. 2004). ATP was extracted from frozen samples in ice-cold 3% perchloric acid, followed by sonication and centrifugation for 2 min at 15 000*g*. Samples were then neutralized, and ATP content was determined (per 10^6 spermatozoa) by quantifying bioluminescence following addition of luciferin–luciferase.

Body condition

We calculated two measures of male body condition: (*i*) Fulton's condition factor (*K*) as $K = M{\cdot}\mathrm{FL}^{-3} \times 10^5$ (where *M* is mass) and (*ii*) residuals from the regression of log(soma mass) on log(FL). Soma mass was calculated by subtracting the total mass of the testes from body mass so that body and testes masses for each individual would be independent. In all cases, both measures of condition yielded the same results, so we report only the latter. In some cases, we included soma mass and FL as predictor variables in a multiple regression, such that the partial coefficient of soma mass represents body condition (Schulte-Hostedde et al. 2005*b*).

Data analyses

We used both JMP (v. 6.0.3) and R (v. 2.4.1) to analyze mean (or median) ejaculate traits per male. We $\log_{10}$-transformed data for age, FL, Fulton's *K*, and the masses of body, soma, and testes in all analyses to normalize residuals (see Table 1 for descriptive statistics on all measured variables).

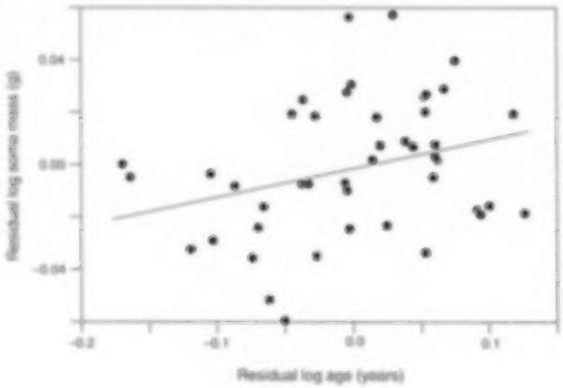
For multiple regression analyses, we first performed hierarchical partitioning analysis (Mac Nally 2000) to choose the most important predictor variables (from testis mass, soma mass, body length, and sperm length) influencing different indices of ejaculate quality (e.g., ATP levels, swimming speed, sperm density). This is an especially useful approach in a study like this where independent variables may be significantly correlated and the sample sizes are relatively small. These selected variables were then entered into a multiple regression analysis of all possible models, and Schwarz's Bayesian information criterion was used to determine the best minimal model in each case. When building models, we considered not only the statistical results but also the biological relevance of each variable. Thus, in the analysis of the different ejaculate traits, we screened for the independent effects of both (*i*) body condition (measured as either residual soma mass or Fulton's *K*) and (*ii*) ejaculate investment (measured as absolute testes mass). In the analysis of sperm ATP, we also included sperm length as a potential independent variable, as longer sperm are expected to require more energy for forward propulsion (Cardullo and Baltz 1991).

Our initial screening of the data indicated three outliers that we removed from subsequent analyses, as follows. First, we removed one male that was by far the oldest fish in our sample (16 years vs. 5–12 years for the rest of the sample) and an exceptionally old fish for this population (J. Casselman, Queen's University, Department of Biology, Kingston, ON K7L 3N6, personal communication). This male was in particularly poor condition for its size, suggesting that it might have been senescent. Second, we excluded one male with unusually small testes for his body size and condition (>3 standard deviations (SD), below the predicted value for this sample), suggesting he may not have been in full breeding condition. Finally, we excluded a male from all analyses involving sperm ATP because his sperm ATP level was particularly low (15.5 pmol·(million sperm)$^{-1}$ vs. 51.5–236.5 for the rest of the sample), indicating that this milt sample had likely thawed before the assay. The removal of these males from analyses resulted in normally distributed residuals and an increase in statistical power (and thus smaller *P* values), but analyses with and without these outliers showed the same patterns.

Results

There was a significant positive relation between log(male age) and log(FL) ($r = 0.69$, $n = 44$, $P < 0.001$). In a multiple regression with log(soma mass) as the dependent variable, there was a significant effect of log(age) (partial $r = 0.29$, $F_{[1,42]} = 3.9$, $P = 0.05$, $n = 45$), with log(FL) held constant.

Fig. 1. Partial regression plot showing relation between body condition (residual soma mass) and age in male lake whitefish (*Coregonus clupeaformis*), with both variables log-transformed and controlling for log(fork length).



Thus the body condition of males improved as they aged from 5 to 12 years (Fig. 1).

As predicted, males in good condition had heavier testes for their body size than males in poor condition, with condition measured as soma mass controlling for body length (partial $r = 0.61$, $n = 47$, $P < 0.0001$; Fig. 2). In a separate multiple regression analysis that included age, body length (FL), and residual soma mass (as an index of condition) as predictor variables (all log-transformed), the effect of age on testes size was not significant ($F_{[1,41]} = 1.4$, $P = 0.25$), but the effects of both residual soma mass ($F_{[1,41]} = 25.8$, $P < 0.0001$) and FL ($F_{[1,41]} = 24.4$, $P < 0.0001$) were both positive and significant. Thus, testis size was influenced by both body size and condition but not by male age.

The best minimal multiple regression model to explain sperm ATP levels included testes mass, body length (FL), and soma mass as predictor variables (Table 2) and explained almost half of the variation in the ATP content of spermatozoa. In this model, sperm ATP levels increased significantly with relative investment in testes (controlling for body length and soma mass) but decreased with body condition (soma mass controlling for body length and testes mass). Thus, larger testes (relative to body size) produced sperm with higher ATP content (Fig. 3*a*), but the production of this ATP, in testes of a particular relative size, appears to have resulted in poorer overall body condition (Fig. 3*b*). Sperm ATP levels were not significantly related to male condition alone (i.e., without controlling for testes mass), with condition measured as soma mass controlling for body length (partial $r = -0.19$, $F_{[1,20]} = 0.30$, $P = 0.59$), though the relation is negative, as in the multiple regression model shown in Table 2.

None of the models predicting sperm density, sperm swimming speed (VAP at 10 s after activation), or sperm motility (percent motile at 10 s after activation) were significant. Thus, these variables were not significantly correlated with male soma mass, FL, sperm length, or testes mass, nor were multiple regressions containing any combination of these variables significant ($P > 0.10$ in each case).

The left testis was larger than the right testis (Table 1) in 38 of 47 males, and this difference (mean = 1.64 g, 95% confidence limit (CL) = 0.71–2.57 g, $n = 47$) is significant within males (paired t test on untransformed data, $t = 3.54$, $P = 0.0009$, $n = 47$). Though left and right testes masses of individual males were correlated (intraclass correlation coefficient = 0.62, $n = 47$), the left testis explained only 38% of variation in the right testis. Interestingly, the size of the left (partial $r = 0.63$, $F_{[1,19]} = 12.3$, $P = 0.002$; Fig. 3*b*) rather than the right testis (partial $r = 0.48$, $F_{[1,19]} = 5.8$, $P = 0.03$) was a better predictor of sperm ATP levels (in both cases controlling for body length and soma mass) in the sample of 23 males for which we measured sperm ATP. Moreover, right testis mass did not contribute significantly (partial $r = 0.28$, $F_{[1,18]} = 1.5$, $P = 0.24$) to a multiple regression model predicting sperm ATP levels from body length, soma mass, and left and right testis sizes, whereas left testis mass did (partial $r = 0.52$, $F_{[1,18]} = 6.6$, $P = 0.02$), suggesting again that the left testis mass was a better predictor of sperm ATP. No other ejaculate traits made a significant contribution to these multiple regression models.

Fig. 2. Relative total testes mass (controlling for body length) in male lake whitefish (*Coregonus clupeaformis*) increases with body condition (soma mass controlling for body length). This partial regression plot illustrates the trend found using multiple regression analysis. In this plot, $y = 3.3 \times 10^{-15} + 3.5x$ ($r = 0.60$, $P < 0.0001$, $n = 47$).

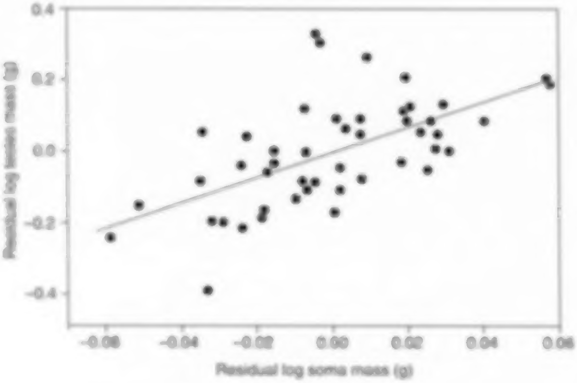


Table 2. Multiple regression model to predict ATP per sperm in lake whitefish (*Coregonus clupeaformis*).

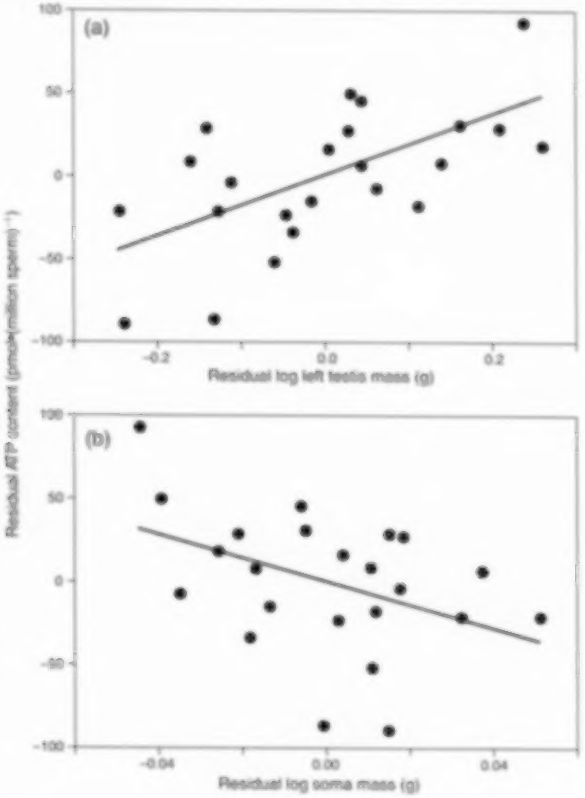
Predictor variable	Standardized Beta	F	P
log(soma mass) (g)	–2.86	10.2	0.005
log(fork length) (mm)	2.2	7.2	0.020
log(combined testes mass) (g)	0.9	12.6	0.002

Note: Whole model: $F_{[3,19]} = 5.11$, $P = 0.009$, $R^2 = 0.45$. The partial regression coefficients (Standardized Beta) indicate both the sign and relative magnitude of each relation when controlling for all other variables in the model.

Discussion

Our results are the first to suggest that individual males investing heavily in testicular tissue also invest differentially in the energetic content of individual spermatozoa. We also found that testis size is asymmetrical in this species, with the left testis larger than the right. Moreover, close to 50% of

Fig. 3. Partial regression plots showing relations between residual adenosine triphosphate (ATP) content of lake whitefish (*Coregonus clupeaformis*) sperm and (*a*) residual mass of the left testis (partial $r = 0.63$, $y = 6.0 \times 10^{-13} + 182.8x$, $P = 0.001$), with both variables controlling for body length and soma mass; and (*b*) residual soma mass as an index of body condition ($r = -0.41$, $y = -2.0 \times 10^{-13} + 700.2x$, $P = 0.05$), with both variables controlling for body length and mass of left testis. Soma mass was calculated as body mass minus combined testes mass in each case. All variables except ATP were log-transformed for these analyses.



the variation in energetic content (ATP levels) of individual spermatozoa was explained by a model that included the size of the left testis, soma mass, and body length. In fact, inclusion of the right testis in that analysis contributed little to the model predicting spermatozoan energy stores. The larger size of the left testis suggests that it produces sperm at a higher rate than the right testis (sensu Scharer et al. 2004). Although such testicular size asymmetry has been reported in birds and frogs (e.g., Møller 1994; Hettyey et al. 2005), we are unaware of any other study that has reported this in fishes. The functional importance of such asymmetry is unclear (Birkhead et al. 1998), but our results suggest that the increased size of the left testis reflects increased investment in the energetic content of spermatozoa, something that has not previously been reported. Møller (1994) argued that directional asymmetry was positively correlated with male quality, but subsequent tests of this hypothesis have yielded equivocal results (Birkhead et al. 1998; Merilä and Sheldon 1999; Hettyey et al. 2005). The discovery of directional asymmetry in lake whitefish and its relationship with sperm energetics indicates that fish may be an appropriate model to test Møller's (1994) hypothesis further.

Why whitefish preferentially invest in one testis is not clear, but the negative relation between sperm energetic content and body condition, holding testis size constant, certainly hints at energetic constraints. Consistent with the presumed costly nature of sperm production (Nakatsuru and Kramer 1982; Olsson and Madsen 1998), we also found a negative relation between sperm ATP content and soma mass, independent of testis mass and body size. This supports the hypothesis that males in good condition before spawning allocate more energy to ejaculates and as a result are in relatively poor condition at spawning (Casselman and Montgomerie 2004). Given the links between sperm energy content and fertilization success detected for other species (e. g., Atlantic salmon, *Salmo salar*; Vladic and Järvi 2001) and the heritability of condition in fish (Kause et al. 2003), females may use ejaculate traits to select for the sperm of males in good condition, thereby exhibiting postcopulatory female choice (e.g., Rakitin et al. 1999). It would therefore be informative to manipulate the condition of individual males to explore the impact on sperm ATP levels, motility, and fertilization success.

A positive relation between testis size and body condition has been reported previously in other taxa (e. g., Simmons and Kotiaho 2002; Schulte-Hostedde et al. 2005*a*), but not, as far as we are aware of, in fishes, even though there are presumably fitness benefits for male fish with relatively large testes. For example, in yellow-pine chipmunks (*Tamias amoenus*), males with relatively large testes had higher annual reproductive success than males with smaller testes (Schulte-Hostedde and Millar 2004). Any positive covariation between ejaculate investment (as indexed by testis size) and body condition would indicate that there may be reproductive benefits accrued by individuals in good condition. Links between condition and reproductive success have been shown previously in whitefish (*Coregonus* sp., Wedekind and Müller 2004) and other fish species (Atlantic cod, *Gadus morhua*; Rakitin et al. 1999), but the physiological mechanisms relating condition and reproductive success are not clear.

ATP stored in spermatozoa prior to ejaculation is probably the primary source of energy for sperm motility in fishes (e.g., Burness et al. 2004). We provide here the first evidence that this sperm energy content is influenced by variation in both body condition and testis size within a population. We suggest two exciting avenues for future work: (*i*) male body condition could be manipulated experimentally to identify the role that body condition plays on sperm energetics, testis asymmetry, and male secondary sexual traits, and (*ii*) the importance of sperm energetics to male fertilization success could be explored. For example, sperm within an ejaculate could be separated based on mitochondrial content using a fluorescence activated cell sorter so that the fertilization success of sperm differing in mitochondrial content could be tested directly. Because our conclusions are necessarily based on correlation analysis, it is impossible to assign cause and effect with complete confidence. This is true of virtually all studies conducted to date on the effects of body condition on ejaculate traits. The results presented here, however, suggest that controlled experiments involving the manipulation of body condition by altering the diet and exercise of male fishes would be a fruitful avenue for further research on ejaculate traits.

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Estimates of juvenile and adult raggedtooth shark (*Carcharias taurus*) abundance along the east coast of South Africa

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Abstract: A Cormack–Jolly–Seber model was developed to estimate abundance, survival, and probability of capture for juvenile (<1.8 m total length, TL) and adult (>1.8 m TL) raggedtooth sharks (*Carcharias taurus*) along the east coast of South Africa. Model estimates were adjusted to account for tag loss, nonreporting, and after release mortality. The model was constructed using mark–recapture data from the Oceanographic Research Institute and Port Elizabeth Museum cooperative tagging programs from 1984 to 2004. The adjusted estimate for juvenile survival was 0.56 and that for adult survival was 0.89. The adjusted estimate of probability of capture for juvenile sharks ranged from 0.06 to 0.17, while that for adult sharks was from 0.02 to 0.04. The mean annual abundance of juvenile sharks was 6800 (coefficient of variation, CV = 13%) and adult sharks 16 700 (CV = 9%). The accumulated effect of tag loss, nonreporting, and after release mortality were to reduce the overall estimate of juvenile and adult abundance by approximately 50%. The adjusted estimate of population size for both juvenile and adult sharks over the last decade appears to have remained constant ($P > 0.05$).

Résumé : Nous avons mis au point un modèle Cormack–Jolly–Seber pour estimer l'abondance, la survie et la probabilité de capture de requins taureaux (*Carcharias taurus*) jeunes (<1,8 m de longueur totale, TL) et adultes (>1,8 m TL) au large de la côte est de l'Afrique du Sud. Les estimations du modèle ont été ajustées pour tenir compte des pertes d'étiquettes, des captures non signalées et de la mortalité après la remise à l'eau. Le modèle est basé sur des données de marquage–recapture provenant des programmes coopératifs de marquage de l'Oceanographic Research Institute et du Port Elizabeth Museum de 1984 à 2004. Après ajustements, la survie estimée des jeunes requins est de 0,56 et celle des requins adultes de 0,89 et la probabilité estimée de capture des jeunes varie de 0,06 à 0,17 et celle des adultes de 0,02 à 0,04. L'abondance annuelle moyenne des jeunes requins est de 6800 (coefficient de variation, CV = 13 %) et celle des adultes 16 700 (CV = 9 %). L'effet cumulatif des pertes d'étiquettes, des captures non signalées et de la mortalité après la remise à l'eau réduit l'estimation globale de l'abondance des jeunes et des adultes d'environ 50 %. La taille estimée après ajustements de la population de requins jeunes et adultes semble être demeurée constante ($P > 0,05$) au cours de la dernière décennie.

[Traduit par la Rédaction]

Introduction

Carcharias taurus is a wide-ranging coastal species of shark found primarily in warm-temperate and tropical waters around the main continental landmasses, except in the eastern Pacific Ocean off North and South America (Last and Stevens 1994; Compagno 2001). In South Africa it is commonly known as the raggedtooth shark, but is also referred to as the sand tiger shark in America and as the grey nurse shark in Australia. It is a long-lived species with an estimated longevity of up to 40 years (Goldman 2002). Female sharks reach sexual maturity at 10 years (Goldman 2002) and exhibit a biennial reproductive cycle (Branstetter and Musick 1994; Lucifora et al. 2002; Dicken et al. 2006*b*). Adelphophagy results in a maximum fecundity of two pups per litter after a gestation period of approximately 9–12 months (Bass et al. 1975; Gilmore et al. 1983). These life history characteristics make this species particularly susceptible to over-exploitation. Declines have been reported in the northwestern Atlantic (Musick et al. 1993, 2000), the southwestern Atlantic (Lucifora et al. 2002), and off the east coast of Australia (Otway et al. 2004).

In South Africa, *C. taurus* has been occasionally reported from the west coast, but is more commonly found along the east coast from Cape Town to northern KwaZulu-Natal (Bass et al. 1975; Smale 2002; Dicken et al. 2006*b*). In response to declining population trends worldwide and the lack of any information on the status of the stock, this spe-

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cies was decommercialised in South Africa through the Marine Living Resources Act in 1998. Although protected from commercial fishing, two fisheries in which *C. taurus* are regularly caught are the bather protection nets of the Natal Sharks Board (NSB), (Wallet 1983; Dudley and Cliff 1993; Dudley 2002) and the competitive shore angling fishery (Smale 2002; Dicken et al. 2006*a*, 2006*b*). Many of the sharks caught in these fisheries are tagged and released as part of the Oceanographic Research Institute and Port Elizabeth Museum cooperative tagging programs. Mark–recapture data from these tagging programs have been used to gain a better understanding of the movement patterns of *C. taurus* in South Africa (Dicken et al. 2007).

The few attempts at assessing shark stocks have produced questionable results because of insufficient data or the use of statistical models that incorporate invalid assumptions (Anderson 1990). Long-term time series of catch and effort data are seldom available for shark species, particularly for those that are not exploited commercially, such as *C. taurus*. As a result, traditional yield-per-recruit models (Grant et al. 1979 for the school shark (or tope), *Galeorhinus galeus*; Smith and Abramson 1990 for the leopard shark, *Triakis semifasciata*) or age- and size-structured approaches (Wood et al. 1979 for spiny dogfish, *Squalus acanthias*; Punt and Walker 1998 and Punt et al. 2000 for the school shark, *Galeorhinus galeus*) are not applicable. Anderson (1990), in discussing fishery models as applied to elasmobranchs, suggested alternative methods such as mark–recapture as a means to obtain estimates of absolute abundance. Mark–recapture models can be broadly defined as either open or closed. Closed population models assume that the population is closed to any additions or removals, such as births, deaths, emigration, or immigration, whereas open models allow for these changes (Williams et al. 2001; Pine et al. 2003). These models, however, have seldom been applied to shark species because of a lack of appropriate biological or fisheries input data. They have been limited to only a few studies, all of which have assumed that the population is closed (Cliff et al. 1996 and Strong et al. 1996 for white sharks, *Carcharodon carcharias*; Campana et al. 1999 for porbeagles, *Lamna nasus*).

There are several approaches to modeling open populations. The Jolly–Seber (JS) model (Jolly 1965; Seber 1965) is a fully open population model that incorporates estimates of recruitment of new animals to the population to estimate population size. *Carcharias taurus*, however, is caught and tagged by volunteer anglers on an ad hoc basis, and not all sharks that are caught are tagged. As a result, the JS model is not applicable. An alternate, yet more restricted model is the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Lebreton et al. 1992; Williams et al. 2001). This model follows only marked animals over time allowing only survival and probability of capture (and not recruitment) estimation. While less general, this model facilitates an adjustment (for model violations) to apparent capture and survival rates, which can then be used to estimate abundance. The objective of this study was to use the CJS model incorporating the tagging data from the Oceanographic Research Institute and Port Elizabeth Museum cooperative tagging programs to estimate the population size of juvenile (<1. 8 m total length, TL) and adult (>1.8 m TL) *C. taurus* along the South African east coast. Information on the population size of *C. taurus* in South Africa is essential in determining its protected status and the validity and effectiveness of the current protective legislature. A review of the literature suggests that this is one of the first applications (see Meekan et al. 2006) of an open capture–recapture population model to any shark species worldwide.

Model development

Tagging

Four different tag types (A-, B-, C-, and D-type) have been used to tag *C. taurus* by members of the cooperative tagging programs. A-type, B-type, and D-type tags are Hallprint manufactured dart tags and are composed of a monofilament vinyl streamer attached to either a plastic barb (A- and D-type) or stainless steel pointed head (B-type). C-type tags are locally manufactured plastic disk tags, similar in design to the Jumbo Rototag. This tag is composed of two plastic disks (a male and female component) that are placed on either side of the hole and then clipped together. Sharks are caught and tagged using three different techniques. They are tagged underwater by scientific divers, from captures in the bather protection nets of the NSB and by shore anglers.

Sharks were tagged and recaptured along the entire east coast of South Africa. A detailed account of tagging localities and areas of recaptures is provided in Dicken et al. (2007). A summary of the environmental characteristics and processes operating along the South African coast is provided in Dicken et al. (2006*a*).

Model assumptions and data requirements

The CJS model has the following assumptions (Pollock et al. 1990): (1) all animals present at sample time i have the same probability of being captured; (2) all animals immediately after sampling have the same probability of surviving to sample time $i + 1$; (3) no tags are lost or overlooked; (4) all animals are released immediately after the sample, and all sample periods have a short duration (relative to time intervals between tagging periods); (5) all emigration from the sample area is permanent and indistinguishable from death; and (6) the survival and capture of an individual is independent of the survival and capture of all other animals.

Estimating the abundance of *C. taurus* is problematic because its complex stock structure and the various methods in which sharks were tagged and released result in a violation of some of the model assumptions. These violations need to be accounted for in the development of the CJS model to avoid bias in the estimates of survival, probability of capture, and abundance. First, the *C. taurus* population is distinctly segregated according to size with a well-defined nursery area (Dicken et al. 2006*b*). Recaptures of tagged sharks (Dicken et al. 2007) have revealed that pups and juvenile sharks <1.8 m TL within the nursery areas display moderate to high site fidelity and do not mix throughout the adult population. As a result, this component of the population is not subject to catches within the bather protection nets of the NSB, as are the adult sharks, yet have a higher probability of capture by shore anglers. These factors lead to heterogeneity in capture probabilities and a violation of the models first assumption. Capture probabilities between individual sharks, within each size class, however, were assumed to be independent and homogenous. This assumption was based on catch records (Dicken et al. 2006*a*, 2006*b*).

Second, anglers' responses to a series of questions regarding the treatment and release time of the "last raggedtooth shark" they caught (Dicken et al. 2006*a*) suggested that a proportion of the sharks that are caught and subsequently released alive suffer size-class-specific after release mortality violating assumption 2. Third, results of a double tagging experiment (Dicken et al. 2006*c*) indicated a clear violation of assumption 3 (i.e., that no tags are lost). Fourth, unlike most mark–recapture experiments, this study revolves around a cooperative tagging program. As a result, sharks are tagged randomly throughout the year and not during well-defined sampling periods, as stated in assumption 4. Furthermore, the majority of tag recaptures are made not by the investigator, but by volunteer anglers. This factor introduces an element of nonreporting, which was investigated in an independent tag-reporting study (Dicken et al. 2006*c*).

Software (SURGE by Pradel and Lebreton 1991, MARK by White and Burnham 1999) has been developed to assist in CJS model-fitting and selection. Unfortunately, the unique features of this study, most notably after release mortality (ARM), tag loss (loss of tag, LT), and the nonreporting of tag recaptures (NR), make a simple model fit using these models inappropriate. As a result, a raggedtooth shark-specific CJS model was developed that was able to incorporate the complexities specific to this study.

Model construction

The design protocol follows that of traditional CJS studies, in which capture histories are summarized into an $\mathbf{m}_{hi}$ array (Lebreton et al. 1992; Williams et al. 2001).

Notation

The notation for the CJS model has been relatively well-standardized (Cormack 1964; Lebreton et al. 1992; Williams et al. 2001). Additional notations (Table 1) have been added as a result of the development of the model in this study.

Likelihood

The CJS likelihood for marked recaptures can be expressed in terms of the statistics (r_i, m_i, z_i), which are calculated from the recapture matrix ($\mathbf{m}_{hi}$). Following Cormack (1964), Seber (1982), and Schwarz and Arnason (1996), the likelihood can be written as follows:

$$(1)\qquad L_{\mathrm{CJS}} = \prod_{i=1}^{s-1}\binom{R_i}{r_i}(1-\chi_i)^{r_i}\,\chi_i^{R_i-r_i}\prod_{i=2}^{s-1}\binom{m_i+z_i}{m_i}\times\left(\frac{p_i}{1-q_i\chi_i}\right)^{m_i}\left(1-\frac{p_i}{1-q_i\chi_i}\right)^{z_i}$$

Incorporation of NR, LT, and ARM

The CJS model does not distinguish how deaths accrue to marked animals in the population. If animals lose their tags, then the observed recaptures will be smaller than expected, and estimates of survival will be underestimated (Arnason and Mills 1981; McDonald et al. 2003). Pollock et al. (1990) extrapolated this conclusion to tag-induced mortality, which reduces the number of marked sharks being returned to the population. Similarly, capture probability will be underestimated if not all tag recaptures are reported to the relevant tagging authority. The effects of all of these problems lead to too few tagged fish being recovered, with a positive bias on the estimation of population size. These effects are most pronounced when capture probabilities are low and fewer tags are available for recapture (McDonald et al. 2003).

Under the situation of LT, the estimated probability of survival will, in effect, be a compounded parameter:

$$(2)\qquad \phi_i = \bar{\phi}_i\Lambda$$

where $\bar{\phi}_i$ is the actual survival probability, and Λ is the tag retention rate between sample i and sample $i+1$. The actual survival probability can therefore be obtained from the compounded parameter as $\bar{\phi}_i = \phi_i/\Lambda$. Likewise, the actual probability of capture is obtained from the compounded estimate as

$$(3)\qquad \bar{p}_i = p_i/\Psi$$

where $\bar{p}_i$ is the actual capture probability, and Ψ is the reporting rate.

In an ideal situation, the effects of capture and tagging will not influence the survival of the marked animal. In reality, however, particularly with large animals that are caught using rod and line or in nets, there will inevitably be some form of ARM. In this situation, the number of marked animals released after the *i*th sample (tm$_i$) need to be reduced by subtracting the number of animals estimated to suffer ARM (d_i).

LT was incorporated statistically into the CJS model through the explicit estimation of LT from data collected in a concurrent double tagging study (Dicken et al. 2006*c*). The LT extension used is based on the maximum likelihood approach (Kirkwood and Walker 1984; Hampton 1997; Adam and Kirkwood 2001). This approach is advocated for use with small data sets in which the number of recaptured fish and the number of fish that have shed a tag are low.

Following Hampton (1997) and Adam and Kirkwood (2001), the probability of a tag being retained at time t is given by

$$\Lambda(t) = \exp(-\lambda t)$$

where λ the tag shedding rate. The probability of a fish retaining one ($P_1'(t)$) or two ($P_2'(t)$) tags after release, conditional on retaining at least one tag at time t, is given by

$$P_1'(t) = \frac{2\Lambda(t)[1-\Lambda(t)]}{1-[1-\Lambda(t)]^2}$$

and

$$P_2'(t) = \frac{\Lambda(t)^2}{1-[1-\Lambda(t)]^2}$$

If n fish are recaptured and reported to have retained at least one tag, indicator variables for the recovery of either one or two tags are given by $N_i^{(2)} = 0$, $N_i^{(1)} = 1$; and $N_i^{(2)} = 1$, $N_i^{(1)} = 0$, respectively.

The likelihood, conditional on recapture times $\{t_i,\ i = 1, 2, \ldots, n\}$, is

$$L_{\mathrm{tag}} = \prod_{i=1}^{n_{\mathrm{tags}}} P_1'^{N_i^{(1)}} P_2'^{N_i^{(1)}}$$

Table 1. Model notations for the development of a raggedtooth shark (*Carcharias taurus*) specific Cormack–Jolly–Seber model.

Statistics	
s	Number of sample occasions.
$\mathbf{m}_{h,i}$	Number of marked animals caught in *i*th sample last caught in sample *h*
n_i	Total number of animals captured at same time *i* (estimated from the angler survey in Dicken et al. 2006*a* and from captures in the shark nets)
u_i	Total number of unmarked animals captured at sample time *i*
m_i	Total number of marked animals reported captured at sample time *i*
mm_i	Number of u_i subsequently newly marked at sample time *i*; not all sharks captured are marked, therefore $\mathrm{mm}_i < u_i$
tm_i	Number of marked animals released (m_i + mm_i) at sample time *i*
d_i	Number of tm_i that suffer after release mortality ($d_i = \mathrm{tm}_i \times \mathrm{ARM}$)
R_i	Number of marked animals released after the *i*th sample ($R_i = \mathrm{tm}_i - d_i$)
r_i	Number of marked animals from the release of R_i animals, which are recaptured later in the experiment
z_i	Number of marked animals caught before sample *i* not captured in sample *i* and captured after sample *i*
ARM	Percentage of sharks that suffer after release mortality
Parameters	
p_i	Probability of capture at sample time *i*
ϕ_i	Apparent survival (1 – mortality – permanent emigration) from sample *i* to *i* + 1
Functions of parameters	
χ_i	Probability of a release not being recaptured after sample *i*; a recursive relationship exists for calculating the probability χ_i where (eq. 4) $\chi_i = \begin{cases} 1 & i = s \\ 1 - \phi_i(1 - q_{i+1}\chi_{i+1}) & i < s \end{cases}$ and $q_i = 1 - p_i$
$\hat{M}_i$	Estimated number of marks in the population: $\hat{M}_i = \dfrac{m_i + z_i}{1 - \hat{q}_i\hat{\chi}_i}$
$\hat{N}_i$	Small sample estimated size of the total population prior to sample *i*: $\hat{N}_i = \dfrac{(\hat{M}_i + 1)(n_i + 1)}{(m_i + 1)}$

The tag-loss-extended CJS model now has an additional likelihood component. The total likelihood to be maximized is expressed as $L = L_{\mathrm{CJS}} \times L_{\mathrm{tag}}$. In this approach, the survival probabilities $\tilde{\phi}_i$ (eq. 2) are estimated together with the LT rate λ, such that the tag-loss-adjusted ϕ_i is included in calculating χ_i and the likelihood (eqs. 4 and 1). In this study, a variety of different tag types and capture methods were used to tag sharks. LT, however, was only estimated for sharks tagged with B-type tags by shore anglers (Dicken 2005). Tag-specific LT rates could not be estimated for the other tag types and tagging methods used in the study, because of a lack of data.

NR was included into the model by adjusting $\tilde{p}_i$ (eq. 3) by the reporting rate. The NR-adjusted p_i is included in calculating χ_i and the likelihood (eqs. 4 and 1).

ARM was included in the model by adjusting the number of released animals by $R_i = \mathrm{tm}_i(1 - \mathrm{ARM})$.

Simulation study

The performance of the CJS estimator was assessed using Monte Carlo simulations, whereby capture histories were generated using a modified version of GENCAPH1, a C-based recursive capture history generation program (www.mbr-pwrc.usgs.gov/software.html). The modified program included both LT and NR as additional forms of survival and capture probability, respectively.

Each simulation was for a five sampling period experiment with temporally invariant parameters. Various combinations of capture probability, survival probability, tag retention, and reporting rates were considered. In total, nine combinations within three simulation scenarios were tested. A total of 500 Monte Carlo simulations were conducted per scenario.

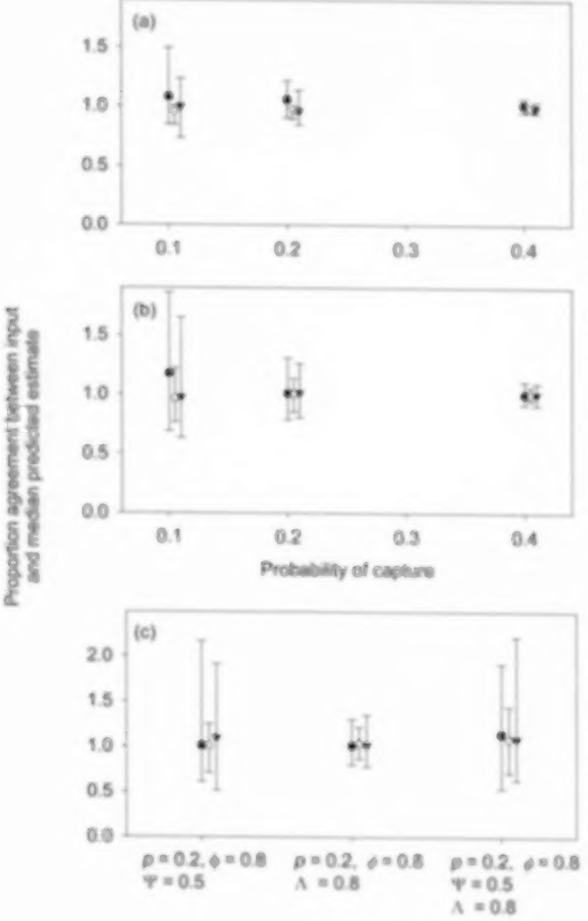
For the first two scenarios, no LT and complete reporting was considered for three different capture probabilities (p_i = {0.1,0.2,0.4}) and two survival probabilities (ϕ_i = {0.8,1.0}). As was to be expected, median-predicted CJS estimates of p_i, ϕ_i, and N_i were similar to the input parameter values (Fig. 1). For both ϕ_i scenarios, the confidence in all the estimated parameters increased with increasing estimates of p_i.

The third scenario included LT and NR with a tag retention rate of Λ = 0.8 and a reporting rate of Ψ = 0.5 (Fig. 1). Median-predicted CJS estimates of p_i, ϕ_i, and N_i were also similar to the input parameter values but were more variable, particularly with the inclusion of the reporting rate, as it in effect halved the probability of capture.

Estimation of parameter variance

Analyses were conducted using AD Model Builder (Otter Research Ltd. 2000), with parameter estimates obtained through nonlinear minimization of the negative logarithm of each respective likelihood function. Estimates of parameter variability are calculated from the inverse Hessian matrix. This approach assumes that the parameter values are asymptotically normally distributed and involves replacing the log-likelihood surface at the maximum likelihood solution by the

Fig. 1. A simulation study to assess the performance of the modified Cormack–Jolly–Seber model to different levels of tag loss and nonreporting. Panels (*a*) and (*b*) assume that all tags are retained and all tagged fish are reported on capture when ϕ is 1.0 and 0.8, respectively. Panel (*c*) illustrates different scenarios of 50% reporting and 20% tag loss. *p* (solid circles), capture probability; ϕ (open circles), survival probability; Λ, tag retention; Ψ, reporting rate. *N* (solid, inverted triangles), population estimate.



quadratic form of the Hessian. The standard errors of $\hat{N}_i$ were calculated using the delta method.

Model selection

Various model configurations were chosen to represent a suite of choices for capture probability (p_i) and survival (ϕ_i) (Table 2). For brevity, they will be referred by model number in the text. The full model, in which p_i and ϕ_i are both time dependent, has 40 estimated parameters. Nested submodels of the full model were specified by estimating common parameters for both p_i and ϕ_i (Hilborn and Mangel 1997). Models 2 and 3, in which $p(t)$ and $\phi(t)$ were set to values before 2001 and after 2001, respectively, reflected the change in shore angling fishing effort with the implementation of a vehicle beach ban in 2001. To reflect a reduction in the number of sharks killed in the nets and the beginning of a catch and release ethic among shore anglers in the early 1990s, $\phi(t)$ was varied before and after 1990 in models 4 and 7. All models were tested for possible overdispersion, also known as extrabinomial variation, using a parameteric bootstrap approach as advocated by Burnham et al. (1987). As there was little evidence for overdispersion ($P > 0.05$ for all models), Akaike's information criteria (AIC) was chosen as a model comparison statistic to determine the most parsimonious model (Burnham and Anderson 2002).

Model application

The data analysed in this study consists of released and recaptured *C. taurus* collected between 1984 and 2005. Tag releases and recoveries were analysed over 12-month periods from the onset of pupping in September each year to the following year. If a shark was tagged as a juvenile but recaptured as an adult, it was included in the adult data set. Because of the distinct spatial segregation of juvenile and adult *C. taurus* (Smale 2002; Dicken et al. 2006*b*, 2007), only adult sharks are susceptible to the bather protection nets of the NSB. There are also differences in ARM rates between the two size classes (Dicken et al. 2006*a*). For these reasons, the CJS model was fitted to both data sets separately as well as to a combined data set. Only 14 sharks were tagged as juveniles but recaptured as adults over the 20-year study period. Owing to a lack of information on the transition between life history stages, it was not possible to model juvenile and adult captures simultaneously using a multistate model.

A summary of the input data, estimated from previous studies, which were utilized in the construction of the CJS models, are provided (Table 3). NR rates for recaptured tagged fish improved markedly from 0.8 in 2001–2002 to 0.33 in 2003–2004 (Dicken et al. 2006*c*). As a result, it was considered appropriate to adjust CJS model estimates with a NR rate of 0.33 for the sampling occasions 2003–2004 and 2004–2005 and a NR rate of 0.5 for all sampling occasions prior to this period. A value of 0.5 is commonly used in tagging studies as a realistic estimate of NR rate (Denson et al. 2002). This value was considered more appropriate than 0.8 because of the uncertainty in the estimation of reporting rates prior to 2003–2004.

The number of sharks caught at each sampling period (n_i) were a product of known captures in the bather protection nets of the NSB (Fig. 2) and an estimated number caught by shore anglers (Table 3). It is important not to misinterpret the catch trends in Fig. 2. The NSB has gradually reduced the number of netted beaches, particularly in recent years, from 39 km in 1999 to 27 km in 2004. As a result, catches in the nets, given net reduction, have in fact remained relatively constant and should not be interpreted as a sign of a decreasing abundance.

Results

Tag shedding

In all, 108 *C. taurus* were double tagged between 2002 and 2004, of which 17 were recaptured (Table 4).

Table 2. Hierarchical model configurations and the number of estimated parameters used in this study.

Model	Parameter configuration	No. of parameters
1	$p(\cdot)\phi(\cdot)$	2
2	p(1984–2000, 2001–2004)$\phi(\cdot)$	3
3	p(1984–2000, 2001–2004)ϕ(1984–2000, 2001–2004)	4
4	p(1984–2000, 2001–2004)ϕ(1984–1990, 1991–2004)	4
5	$p(\cdot)\phi(t)$	21
6	$p(t)\phi(\cdot)$	21
7	$p(t)\phi$(1984–1990, 1991–2004)	22
8	$p(t)\phi(t)$	40

Note: The (t) and ($\cdot$) notation signify time dependence and independence, respectively.

Table 3. Estimates of shore angling catch (SC) (Dicken et al. 2006*a*), after release mortality (ARM) (Dicken et al. 2006*a*), and nonreporting of tag recaptures (NR) used in the development of unbiased juvenile (<1.8 m total length, TL) and adult (>1.8 m TL) *Carcharias taurus* Cormack–Jolly–Seber models.

Bias adjustment	Juvenile model	Adult model
SC	1120	643
ARM	0.04	0.22
NR	0.5 (before 2003–2004), 0.33 (after 2003–2004)	

Model selection

The model comparison statistics for a combined data model and an aggregate model (combining separate juvenile and adult models) are provided (Table 5). Modelling the juveniles separately from adults resulted in a most parsimonious model, as AIC for the aggregated model (model 2 juvenile + model 2 adult) was 2660 compared with 2694 for model 2 of a combined data set. The most parsimonious model for either the juvenile or adult life history stages was model 2, where p(1984–2000, 2001–2004)$\phi(\cdot)$.

Parameter estimates in the following sections are provided only for the selected best model (model 2) for both the juvenile and adult data sets. The predicted number of tag recaptures showed good agreement with the observed number of juvenile and adult sharks (Fig. 3), suggesting that the model was not misspecified.

Survival and probability of capture

The estimates of parameters for the juvenile and adult models are provided (Table 6). The estimate of p_i for juvenile sharks increased markedly after 2001, from 0.12 to 0.17. In contrast, p_i for adult sharks remained relatively constant. The estimates of $p_{1984-2000}$ and $p_{2001-2004}$ for juvenile sharks were 3.5 and 5 times greater, respectively, than those for adult sharks. The higher estimate of ϕ_i for adult (0.69) compared with juvenile (0.43) sharks was not surprising. Estimates of survival, however, are apparent and not true survival; for apparent survival to be true survival, emigration must not occur (Pollock et al. 1990). In this study, juvenile sharks effectively emigrate from the juvenile population when they reach a TL of 1.8 m and become part of the adult population. As a result, the juvenile estimate of survival is an underestimate of true survival. Apart from a possible movement into Mozambique waters, emigration of adult sharks from the South African population is negligible. Consequently, the survival estimate for adult sharks is a reasonable approximation of true survival.

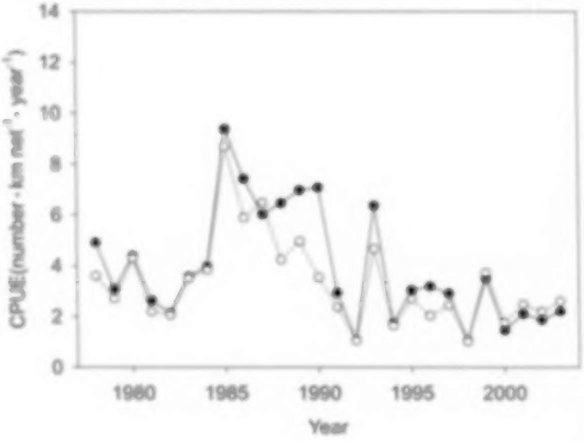


Fig. 2. Annual catch per unit of effort (CPUE) (solid line, solid circles) of *Carcharias taurus* caught in the bather protection nets of the Natal Sharks Board between 1978 and 2003 for all installations excluding Richards Bay, Mzamba, and the months of June and July, which encompass the sardine run (*Sardinops sagax*) (broken line, open circles).

Adjustments were made to estimates of both p_i and ϕ_i to correct for bias resulting from ARM, LT, and NR. ARM increased estimates of both p_i and ϕ_i slightly; as adult sharks suffered greater ARM than juvenile sharks, the parameter adjustments were greater. Tag shedding also resulted in positive adjustments to estimates of ϕ_i. A 50% and 33% time-dependent tag NR rate increased estimates of p_i by 100% and 30%, respectively.

Owing to the difficulties in directly estimating natural mortality rates in sharks, a number of indirect methods have been developed. Five methods were chosen: Hoenig (1983); Peterson and Wroblewski (1984); Chen and Watanabe (1989); Jenson (1996); and Cortés (2000); and these were used to obtain comparative estimates of survivorship (S = exp($-M$)) (Table 7). Von Bertalanffy parameters from Goldman (2002) were used in each of the five methods, as

Table 4. Numbers of recoveries and times at liberty of originally double-tagged juvenile (<1.8 m total length, TL) and adult (>1.8 m TL) *Carcharias taurus* retaining one or two tags on recapture.

Days at liberty	No. of recoveries	
	One tag	Two tags
28	0	1
81	0	1
226	0	1
277	0	1
285	0	1
327	0	1
337	1	0
364	0	1
439	0	1
631	0	1
636	0	1
242	0	1
400	1	0
481	1	0
647	1	0
669	1	0
744	1	0

Note: Data have been pooled for both life history stages.

was the value of t_{max} (40 years). For the Peterson and Wroblewski (1984) method, weights-at-age were determined by calculating TL at age from the von Bertalanffy growth function and then converting these values into weight using the length–weight regression relationship in Dicken et al. (2006*b*). Two methods that give age-dependent values are those of Peterson and Wroblewski (1984) and Chen and Watanabe (1989). Since juvenile survival rates estimated from the model include emigration, estimates of survival rate from these indirect methods are only comparable for adult sharks. The adult estimate of survival was calculated using an age of 20, which was considered an approximate midpoint for the life expectancy of this age class. In the absence of commercial exploitation, total mortality (*Z*) estimated in the Hoenig (1983) calculation can be viewed as an approximate estimation of natural mortality (*M*).

Abundance

Estimates of juvenile and adult population abundances (including adjustments to incorporate ARM, LT, and NR) for the 20-year study period are illustrated (Fig. 4). The original, unadjusted, annual population estimate for juvenile sharks ranged from 4300 (1987–1988) to 8500 (1995–1996). The overall estimate for the 20-year study period was 6800 (CV = 13%). The unadjusted annual estimate for the abundance of adult sharks was almost three times greater than that of juvenile sharks and ranged from 9000 (1985–1986) to 25 000 (1991–1992). The overall estimate for the 20-year study period was 16 700 (CV = 9%). The greater number of adult compared with juvenile sharks was expected, considering juvenile sharks consisted only of the age classes 0 to 4, while adult sharks incorporated all subsequent age classes to the life expectancy of 40 years. Confidence intervals for estimates of both juvenile and adult abundance were fairly wide, which results from the small number of tag recaptures, particularly in the first half of the study period.

ARM, LT, and NR all adjusted estimates of abundance negatively. NR was the biggest source of bias for estimates of both juvenile and adult abundance. The effect of ARM and LT were both more pronounced for adult sharks because (*i*) adult sharks suffered greater ARM than juvenile sharks and (*ii*) the effect of LT on estimates of abundance is more

Table 5. Model fits for juvenile (<1.8 m total length, TL) and adult (>1.8 m TL) *Carcharias taurus* Cormack–Jolly–Seber estimators and a combined data estimator sampled from 1985–1986 to 2003–2004, based on probability of capture and survival.

Data set	Model	κ	–ln*L*	AIC
Juvenile	1	2	443.04	890.1
	2	3	441.54	889.1
	3	4	441.19	890.4
	4	4	441.41	890.8
	5	21	428.02	898.0
	6	21	431.87	905.7
	7	22	431.85	907.7
	8	40	423.68	927.3
Adult	1	2	884.72	1773.4
	2	3	882.72	1771.4
	3	4	881.92	1771.8
	4	4	882.36	1772.7
	5	21	874.14	1790.3
	6	21	877.02	1796.0
	7	22	877.01	1798.0
	8	40	867.34	1814.7
Combined data	2	3	1344.50	2695.0
Juveniles separate from adults	2	6	1324.28	2660.5

Note: κ indicates the number of estimated parameters; –ln*L* is the log likelihood; AIC is the Akaike's information criterion measuring model fit as AIC = –2 ln*L* + 2κ.

Fig 3. The observed (circles) and Cormack–Jolly–Seber predicted number of tag recaptures ($\hat{M}_i\hat{p}_i$) (lines) for juvenile (solid circles) (<1.8 m total length, TL) and adult (open circles) (>1.8 m TL) *Carcharias taurus* sampled from 1985–1986 to 2003–2004.

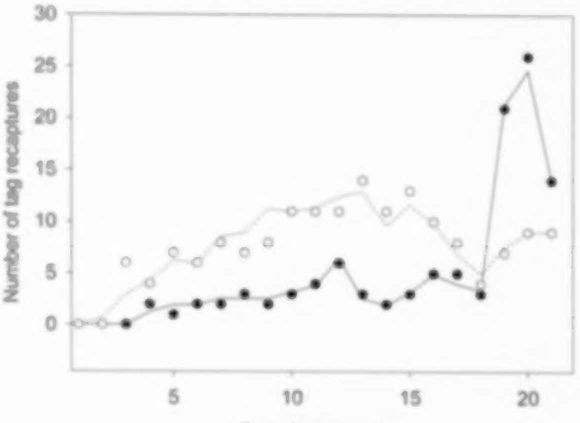


Table 6. Maximum likelihood estimates and their coefficients of variation (in parenthesis) for capture probabilities (p_i), survival rates (ϕ_i), and tag loss rate (λ) for juvenile (<1.8 m total length, TL) and adult (>1.8 m TL) *Carcharias taurus* from model 2, p(1984–2000, 2001–2004)ϕ(•).

	$p_{1984\text{–}2000}$	$p_{2001\text{–}2004}$	ϕ_i	λ
Juveniles				
Unadjusted	0.12 (21.95%)	0.17 (18.3%)	0.43 (10.16%)	—
LT	0.12 (21.95%)	0.17 (18.3%)	0.55 (15.24%)	0.25 (46.32%)
ARM	0.12 (21.85%)	0.17 (18.21%)	0.43 (10.07%)	—
NR	0.06 (21.91%)	0.09 (18.04%)	0.44 (10.00%)	—
LT + ARM + NR	0.06 (21.82%)	0.09 (17.93%)	0.56 (15.08%)	0.25 (46.32%)
Adults				
Unadjusted	0.03 (12.38%)	0.03 (21.92%)	0.69 (3.36%)	—
LT	0.03 (12.38%)	0.03 (21.92%)	0.89 (11.85%)	0.25 (46.32%)
ARM	0.04 (12.22%)	0.04 (21.85%)	0.70 (3.27%)	—
NR	0.02 (12.37%)	0.02 (22.02%)	0.69 (3.37%)	—
LT + ARM + NR	0.02 (12.21%)	0.02 (21.96%)	0.89 (11.83%)	0.25 (46.32%)

Note: Bias corrected estimates to account for tag loss (LT), after release mortality (ARM), and nonreporting of tag recaptures (NR) are also presented.

Table 7. Indirect estimates of natural mortality (M) and survivorship (S) for adult *Carcharias taurus*.

Citation	Method	M	S (%)
Hoenig 1983	$\ln(Z) = 1.44 - 0.982x\ln(t_{\max})$	0.11	89.34
Peterson and Wroblewski 1984	$M = 1.92W^{-0.25}$	0.11	89.75
Chen and Watanabe 1989	$M_{(t)} = \dfrac{K}{\exp[-\{k(t - t_0)\}]}$	0.12	88.38
Jenson 1996	$M = 1.6K$	0.19	83.06
Cortés 2000	$M = \dfrac{\log_e(0.01)}{t_{\max}}$	0.12	89.13

Note: In the absence of commercial exploitation, total mortality (Z) estimated in the Hoenig (1983) calculation can be viewed as an approximate estimation of natural mortality (M). W, body weight; K and t_0 are von Bertalanffy growth parameters; $t_{\max}$, maximum age.

pronounced when capture probabilities are low (McDonald et al. 2003).

The accumulated effect of ARM, LT, and NR were to reduce the overall estimate of juvenile and adult abundance for the 20-year study period by approximately 50%. Because of the effects of bias on the estimates of abundance, it is perhaps more insightful to examine trends in abundance, rather than the absolute estimates themselves. Trends in abundance were analysed for only the last 10 years, because of the low number of tag recaptures in the first half of the study. Adjusted (ARM, LT, and NR) estimates for juvenile and adult abundance over the past decade exhibited no statistically significant trend (tests of regression slope, $P > 0.05$).

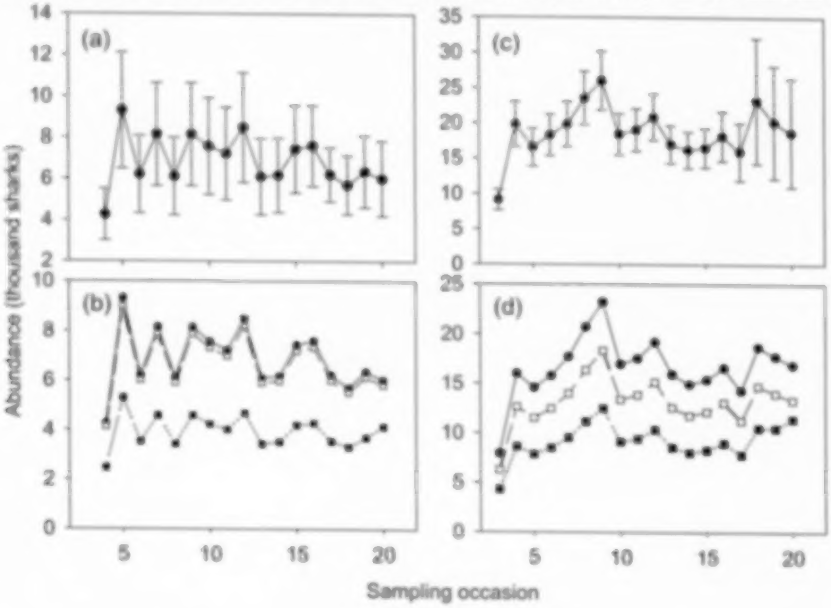
Discussion

The analysis presented in this study represents one of the first applications of an open population mark–recapture model to any species of shark population worldwide (Meekan et al. 2006). The model provides estimates of survival and abundance, which will provide information to support management decisions on a species that is threatened throughout much of its geographical range. The CJS model incorporates information obtained from auxiliary studies on catches (Dicken et al. 2006*a*), stock structure (Dicken et al. 2006*b*), ARM rates (Dicken et al. 2006*a*), NR rates (Dicken et al. 2006*c*), and LT rates (Dicken 2005) to adjust for violation of some of the models assumptions.

The first assumption of the CJS model is that every animal present in the population at sampling time i has an equal probability of capture. Catch data (Dicken et al. 2006*a* and 2006*b*) and tag recapture information (Dicken et al. 2007) have illustrated the distinct spatial segregation of the juvenile and adult population. Each component of the population is subject to regional variation in fishing pressure, as well as different methods of capture. For instance, juvenile sharks are only caught by shore anglers, whereas adult sharks are also caught in the bather protection nets of the NSB. As a result, it was necessary to model juvenile and adult components of the population separately to avoid bias of the equal catchability assumption. A violation of this assumption would result in a negative bias in the estimation of abundance (Pollock et al. 1990).

Like many other studies on shark populations, the results reported in this study must be considered preliminary because of the uncertainty in many of the models' input values. First, there is uncertainty in the capture sample sizes. The crude capture sample sizes estimated from a survey of

Fig. 4. Unadjusted estimates of mean abundance and 95% confidence intervals for (*a*) juvenile (<1.8 m total length, TL) and (*c*) adult (>1.8 m TL) *Carcharias taurus* sampled from 1985–1986 to 2003–2004. Adjusted estimates of abundance to account for tag loss (solid circles), nonreporting of tag recaptures (solid squares), and after release mortality (open squares) for juvenile (*b*) and adult (*d*) populations.



coastal competitive shore anglers (Dicken et al. 2006*a*) had wide 95% confidence limits and was only calculated for the 2002–2003 fishing season, yet applied to the entire study period. Despite the vehicle beach ban in 2001, there was no evidence of a marked reduction in the number of sharks caught compared with previous years. This was as a result of a small core of dedicated competitive anglers who catch the majority of sharks (Dicken et al. 2006*a*). A gross miscalculation in sample size or marked variation in the annual number of sharks caught could result in either an overestimate or underestimate in the calculation of the CJS parameters. Second, there is uncertainty in the estimated number of sharks that die from ARM (Dicken et al. 2006*a*). However, because the numbers that are expected to die are minimal, this uncertainty will have little effect on the estimates of either $\hat{p}_i$ or $\hat{\phi}_i$. The fraction of fish that are expected to suffer ARM is constant over all tagging episodes so there is no effect on the trends in abundance.

In addition to these uncertainties, the CJS estimates of p_i and ϕ_i were corrected to account for bias resulting from NR and LT. While the estimate of ϕ_i was adjusted statistically, the adjustment of p_i was considered ad hoc. Whereas this approach included some additional biological plausibility into the model by including the best available information, it did not adequately estimate parameter variability.

The CJS model that best explained the data for both the juvenile and adult populations was model 2, in which capture probability varied before and after 2001–2002 and survival was constant. In December 2001, the use of vehicles on beaches was prohibited. As a result of the ban, anglers stated that they fished less for sharks and caught fewer *C. taurus* (Dicken et al. 2006*a*). Capture probabilities for adult sharks were similar for both periods ($p_{1984\text{–}2000}$ = 0.03, 95% CI = 0.03–0.04), $p_{2001\text{–}2004}$ = 0.03, 95% CI = 0.02–0.05). In contrast, rather than a decreasing p_i for juvenile sharks, it increased from $p_{1984\text{–}2000}$ (0.12, 95% confidence interval, CI = 0.08–0.17) to $p_{2001\text{–}2004}$ (0.17, 95% CI = 0.12–0.25).

Rather than detecting a change as a result of the beach vehicle ban, the increase in juvenile p_i was probably a reflection of the greater number of juvenile sharks tagged by Port Elizabeth Museum taggers after 2001 (Dicken et al. 2007). The more parameterised models (models 5 to 8), which attempted to reflect changes in the attitudes of fishermen from one of catch-and-kill to a catch-and-release ethic and a gradual reduction in the number of bather protection nets, performed poorly. A possible explanation is that these sources of mortality have had little effect on the survivorship of either the juvenile or adult *C. taurus* populations. Alternately (and possibly more likely), the effects of these changes in fishing pressures have been masked by the relatively small tag–recapture data sets used in this study.

Juvenile and adults sharks had different parameter estimates for both $\hat{p}_i$ and $\hat{\phi}_i$, with juveniles exhibiting higher probabilities of capture and lower probabilities of survival. Juvenile sharks tended to concentrate within rocky reef habitats within the nursery areas and exhibit a high degree of site fidelity (Dicken et al. 2006*b*, 2007). In comparison, adult sharks had a more dispersed distribution pattern extending along the entire coastline, possibly reflecting their wider-ranging movements along the coast (Dicken et al. 2006*b*). Shore anglers had a greater probability of landing juvenile compared with adult sharks, which because of their size and strength allowed them to break tackle and be lost once hooked. As a result of these factors, it was not surprising that the bias-adjusted estimates of p_i for juvenile sharks were three to four times greater than that for adult sharks.

The juvenile estimate of ϕ_j (0.56) adjusted for ARM, LT, and NR is similar to the value (0.48) obtained by Manire and Gruber (1993) for an unexploited population of young-of-the-year lemon sharks (*Negaprion brevirostris*). This estimate, however, as in the current study, is probably an underestimate as a result of emigration of juvenile sharks into the adult population when they reach maturity. The survival estimated here is therefore apparent survival (1 – mortality – emigration) rather than true survival. Unfortunately, the data required to assess the juvenile–adult transition at present is unavailable, and as a result it is not possible to estimate true survival and emigration separately.

Ignoring a negligible movement into southern Mozambique, the adult population of *C. taurus* is closed to emigration. As such, the adjusted estimate for adult survival (ϕ = 0.89), accounting for ARM, LT, and NR, in contrast with that for juveniles, reflects true rather than apparent survival. This estimate is in good agreement with all five of the indirect estimates that ranged from 0.84 to 0.90. Aasen (1963) obtained a similar direct estimate of survival (0.85) for the Porbeagle shark (*Lamna nasus*), a species of similar size and life history characteristics to *C. taurus*.

Owing to the uncertainty in the extent and effect of NR rate and LT on the CJS estimates of abundance, it is perhaps prudent to discuss trends in population sizes rather than absolute estimates. Trends in juvenile and adult abundance for both the unadjusted and adjusted estimates remained relatively constant over the course of the study period. Indications of a healthy population that is more likely to be increasing rather than decreasing are supported by catch rate, size, and population trends evident from catches in the bather protection nets of the NSB (Dudley 2002; Dudley and Simpfendorfer 2006). This information suggests that neither component of the population is being subjected to excessive fishing pressures. The ban on beach driving in 2001, which restricts the ability of the majority of fishermen to catch sharks, combined with a catch and release ethic and a continued reduction in the number of bather protection nets along the coast are all positive indicators that the minimal fishing pressure this species is subjected to will continue to decrease in the future. Of concern, however, is the increased targeting and catch of *C. taurus* by commercial ski boat anglers, in response to a reduction in the number of allotted linefish licences (Dicken et al. 2006*b*). Despite all these factors, the life history characteristics of *C. taurus* make it particularly susceptible to any form of exploitation. Additional mortality, even at low levels for a slow-growing, late-maturing species such as *C. taurus*, could reduce the population growth rate to values of <1.0, resulting in severe population declines in a very short time period (Baum et al. 2003; Otway et al. 2004). As a result, the current protective legislature prohibiting the commercial exploitation of this species should remain in place.

Collaborative tagging programs are the only cost-effective method for studying a species that is not exploited commercially and is only caught recreationally in relatively low numbers. Nevertheless, there are some data quality issues inherent in programs where volunteer anglers do the majority of tagging. Cooperative tagging programs have typically been limited to a simple descriptive analysis of movement patterns. The multimethod approach used in this study to account for stock structure, sample size, tag shedding, and NR and ARM rates could be applied to other tagging programs to estimate critical population parameters for other recreationally exploited species elsewhere in the world.

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Life history and large-scale habitat use of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) — implications for species replacement patterns

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Abstract: Simple models of temperature-mediated interference competition have generally failed to explain salmonid species replacement patterns along altitudinal gradients, a fact that emphasizes the need to link individual features and their relation to habitat characteristics to population-level dynamics. We compared life history parameters in stream-resident populations of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in eight boreal streams. By use of electrofishing data from 1000 sites, we analyzed and related differences in life history traits to habitat- and interaction-related patterns of growth and densities of brook and brown trout, respectively. Brown trout were competitively dominant throughout the size span of sampled sympatric sites and lowered growth rates in sympatry were mainly caused by environmental factors, revealing a link between brook trout invasions and habitat-related limitations on brown trout performance. Still, the frequency of allopatric brook trout sites increased in the smallest watersheds, indicating that localities with a high degree of brook trout dominance rarely sustain brown trout over time. Brook trout populations had higher turnover rates and proportions of mature females than brown trout populations. Our results suggest growth potential and its effect on population fecundity as a critical factor limiting competitive ability and distribution of brown trout in Swedish brook trout dominated headwaters.

Résumé : Les modèles simples de compétition d'interférence par l'intermédiaire de la température n'arrivent généralement pas à expliquer les patrons de remplacement des espèces de salmonidés le long de gradients d'altitude; cela souligne la nécessité de relier les traits individuels et leurs relations aux caractéristiques de l'habitat à la dynamique à l'échelle de la population. Nous avons comparé les variables démographiques de populations d'eau courante d'ombles de fontaine (*Salvelinus fontinalis*) et de truites brunes (*Salmo trutta*) dans huit cours d'eau boréaux. Les données de la pêche électrique à 1000 sites nous ont servi à analyser et à relier les différences dans les caractéristiques démographiques à des patrons de croissance et de densité liés à l'habitat et aux interactions chez chacune des deux espèces. Les truites brunes prédominent dans la compétition sur toute l'étendue des tailles d'habitats sympatriques échantillonnés et la réduction de leur croissance en conditions de sympatrie est causée principalement par les facteurs du milieu; les patrons indiquent un lien entre les invasions d'ombles de fontaine et les limitations imposées par l'habitat à la performance de la truite brune. Néanmoins, la fréquence des sites contenant l'omble de fontaine en allopatrie est plus importante dans les bassins versants les plus petits, ce qui indique que les sites à forte dominance d'ombles de fontaine permettent rarement la persistance de la truite brune dans le temps. Les populations d'ombles de fontaine ont des taux de remplacement et des proportions de femelles matures plus importants que ceux des truites brunes. Nos résultats laissent croire que le potentiel de croissance et son effet sur la fécondité de la population sont des facteurs critiques qui limitent la capacité de compétition et la répartition de la truite brune dans les cours d'eau d'amont dominés par l'omble de fontaine en Suède.

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Introduction

Understanding mechanisms that control species distributions is a central theme in ecological research. Environmental conditions and interactions with other organisms are fundamental structuring factors that determine patterns of distribution and the composition of species assemblages. These factors also interact so that interspecific interactions are modified by the environment in which they occur. Such processes are frequently demonstrated in systems in which the outcome of interspecific competition is altered or reversed by changing environmental conditions, a mechanism referred to as condition-specific competition (Dunson and Travis 1991; Costanzo et al. 2005).

Temperature-mediated changes in competitive superiority are considered an important structuring factor behind the species replacement patterns along altitudinal gradients that are commonly found among stream-dwelling salmonids (e.g., Fausch 1989; De Staso and Rahel 1994; Taniguchi and Nakano 2000). The specific underlying mechanisms by which these changes occur are, however, still poorly understood. Over the last century, salmonid species have been widely spread through man-made introductions. New combinations of species that have not evolved together provide opportunities for intense interspecific competition (Hearn 1987; Fausch 1988), interactions that have had negative effects on native salmonids (Krueger and May 1991). In Sweden, introduced brook trout (*Salvelinus fontinalis*) have been successful in establishing a substantial number of new populations throughout the country, a fact that has raised concerns about indigenous brown trout (*Salmo trutta*) populations becoming extinct (Pakkasmaa and Petersson 2005). According to Nilsson (1967), brook trout have been able to establish populations in small Swedish streams, particularly in cold headwater reaches with a relatively high proportion of groundwater influx. In North America, introduced or invading brown trout have replaced brook trout in lower and middle reaches of many streams, leaving the same patterns of distribution over a stream-size gradient as in Sweden (Fausch and White 1981; Kozel and Hubert 1989; Rahel and Hubert 1991). The displacement of brook trout in lowland streams has been described (Waters 1983), but the underlying mechanisms are not fully understood. Suggestions in the literature include displacement of brook trout from preferred resting or feeding areas (Fausch and White 1981), predation on brook trout by brown trout (Johnson 1981), differences in susceptibility to angling (Marshall and MacCrimmon 1970), and vertebrate predation (Alexander 1976). Limitations on upstream dispersal of brown trout have been attributed to low water temperatures (Gard and Flittner 1974).

Stream-resident forms of brown trout and brook trout have many features in common. Some differences have, however, been suggested, e.g., higher growth rate during the first years and earlier attainment of sexual maturity for brook trout (McFadden and Cooper 1964; Nyman 1970; Jensen 1971). Both species are territorial but there are indications that brook trout are less rigid in their territorial behaviour compared with other salmonids (Newman 1956; Keenleyside 1962). Brown trout on the other hand is renowned for being an aggressive interference competitor that generally dominates other salmonids (e.g., Kalleberg 1958; Dewald and Wilzbach 1992; Hasegawa et al. 2004). Hence, although some results suggest otherwise (e.g., Fausch and White 1986), literature generally suggests brown trout as the more aggressive interference competitor.

Territorial defence and interference competition for suitable microhabitats are considered highly important for the structuring of intra- and inter-specific interactions among stream-dwelling salmonids (Hearn 1987; Nakano 1995; Harwood et al. 2002). Temperature-specific dominance in pairwise contests has been frequently used as a measure of interspecific competitive ability, and several studies have found the dominating species at lower altitudes to be the superior competitor at high temperatures. There is, however, a considerable lack of evidence for reversed interference competitive relationships when water temperatures are lowered (De Staso and Rahel 1994; Taniguchi et al. 1998; Taniguchi and Nakano 2000). It seems as though species' distribution along an altitudinal gradient can not be solely explained by a simple model of condition-specific interference competition without considering mechanistic linkages among behavioural and physiological responses to the environment, resource use, and demographic processes (Taniguchi and Nakano 2000). Hence, the need for a more large-scale approach in which individual features and their relation to habitat characteristics are linked to population-level dynamics has become increasingly evident with time.

Species-specific life history characteristics and their relation to the environment provide the framework within which interspecific interactions can be analyzed and understood. In this study, we used electrofishing and life history data to analyse effects of interspecific competition and to assess differences in life history traits and their potential role in structuring the outcome of interactions on a landscape scale.

For evaluating effects of interspecific competition, we analysed interaction- and habitat-related patterns of growth and densities of brook and brown trout, respectively, using data from the Swedish electrofishing register (SERS). More specifically, we tried to answer the following questions. Are densities and growth of brook and brown trout, respectively, affected by the presence of the competing species? If so, are competitive effects asymmetrical and does that asymmetry change along a stream-size gradient as predicted by the hypothesis of condition-specific competition?

Available information about differences in life history strategies between the two species are almost without exception of North American origin. To allow the assessment of landscape-scale patterns of competitive outcomes and distributions in relation to locally derived information on species-specific differences in life history traits, SERS data was complemented by collection and analyses of life history data from eight mid-Sweden streams. Given the need for alternative mechanistic explanations to the upstream decline of "dominant" salmonids, we included analyses of life history data from brown trout in streams with and without brook trout.

Materials and methods

This study includes analyses of electrofishing data from 1000 sites within SERS and life history data from eight small boreal streams in the central and eastern parts of the county of Jämtland, central Sweden. Large amounts of data over a large geographical range allowed a separation of environmental effects from those of biotic interactions in analyses of SERS data. Hence, this data set was used for analyses regarding the existence and strength of interspecific competition between the two species. Life history data from our field-study streams were used for assessing differences in life history parameters between species, as well as between brown trout populations in streams that have or have not been subject to brook trout invasions.

Field-study streams

Out of the eight streams that were sampled in our field study (Table 1), four had populations of brown trout and four had sympatric populations of brown trout and brook trout.

All streams are widely separated in space, with the two closest streams (Gulån and Färsån) being 12 km apart. These streams run mainly through peat bog areas and boreal woodland dominated by Norwegian spruce (*Picea abies*), scots pine (*Pinus sylvestris*), and birch (*Betula pubescens*). All catchments are dominated by calcium-rich soils, and the altitudinal range of sampled areas is between 225 and 415 m above sea level (a.s.l.). Furthermore, the streams had similar wetted widths (Table 1), reducing the effect of different habitat on fish. Fish species other than brown trout and brook trout are present in low or very low densities, leaving the salmonids as dominating species in all streams. This especially applies for the potential predators burbot (*Lota lota*) and northern pike (*Esox lucius*), which without exception are extremely rare. Fishing pressure is very low in all streams. All populations of brown and brook trout are considered stream-resident, with the exception of Sågbäcken where migratory behaviour is possibly present among some individuals of the brown trout population. Brown trout coexisted with brook trout in all localities sampled in Färsån and Gulån, with a slight numerical dominance of brown trout. In Höglundabäcken and Sågbäcken, the two species were more segregated and the major part of the brook trout sample originated from the uppermost and the middle localities.

Fish data collection

Direct-current electrofishing was performed at three locations in each stream, except in Sågbäcken where four stations were sampled. All stations, each measuring about 100 m in length, were fished in three successive removals. In streams where more individuals were needed for analyses, complementary qualitative sampling was performed. In total, the length of the stream sections that were encompassed in electrofishing surveys varied between 1.2 km and 5 km. All fish were measured to the nearest millimetre (standard length). Age determination was done in a microscope using scales from brown trout and otoliths from brook trout. Sex and status of sexual maturation (Dahl 1917) were determined via dissection for all fish above age 0+, whereas subsamples were used for age-0+ fish. In sexually mature females, fecundity was measured by counting total numbers of eggs. All samplings were performed between 28 August and 7 October 2002. In results from the field study, brown trout populations are labelled sympatric or allopatric based solely on the presence or absence of brook trout. In general, we use the terms sympatric or coexisting populations in the sense that they coexist on a given specific sampled site.

Field-study data analysis

Mortality was estimated by using simple catch curves (Ricker 1975; Vetter 1988) based on summed catches where the slope of the linear regression model on $\log_e$(number) over age gave instant mortality rate for the population. Age-0+ fish were excluded from mortality analyses because of lower catchability and more patchy distributional patterns linked to the location of spawning sites. In Färsån and Krokdalsbäcken, age-1+ fish were excluded because the catch of age-1+ individuals was substantially lower than that of age-2+ trout, indicating that recruitment of the age-1+ cohort was unusually low. For the same reason, age-1+ and age-2+ trout had to be excluded in Gulån. Because of smaller sample sizes, mortality rates were not estimated for brook trout populations. Age at maturity was estimated by using a logistic regression with mature/immature as a nominal, dependent variable (Trippel and Harvey 1991). The regression was expressed as a function $j(x)$, describing the length-specific probability for a female to be sexually mature. The general expression of this function is $j = \frac{1}{1 - e^{-k}}$, where k is a linear expression of the kind $k = (\gamma + \beta_1 N + \ldots)$ in which γ and β_1 are regression coefficients and N is age or length.

In the analysis of proportion of mature females in the total catch, old data (Sundbaum 2001; Hallin 2002) based on externally determined status and sex were included from Gulån, Krokdalsbäcken, and Bjuråsbäcken. In this analysis, two sampled sites from Sågbäcken were excluded because of possible migratory behavior in the brown trout population. Incomplete data sets from Bjuråsbäcken (lacking information on age and fecundity) and Sågbäcken (low number of mature brown trout females and possible migratory behavior in two out of four sampled sites) caused the exclusion of these streams from several analyses, leaving three allopatric and three sympatric streams as part of all analyses. Statistical comparisons between populations in the streams of the field study were done using analysis of variance (ANOVA) or analysis of covariance (ANCOVA) with age, age group, fish species, and stream as fixed factors. Comparisons of means were made using t tests or Wilcoxon tests depending on whether variances differed between populations (tested with F test).

Swedish electrofishing register (SERS)

In SERS, a database containing more than 12 000 studied sites (32 448 fishing occasions) in Swedish streams, standardized electrofishing data are provided by various organizations and authorities. Population densities of different species are calculated according to Bohlin et al. (1989) when electrofishing is made in successive removals. If only one removal is made, densities are calculated from the average catch efficiency of the given species and age class (Degerman and Sers 1999).

At the fishing occasion, water temperature is measured at a midstream depth of 0.3 m. Altitude (m a.s.l.) and latitude are measured from maps to the nearest 1 m and 10 m, re-

Table 1. Data for the streams sampled in the field study (stream, coordinates, altitude (in metres above sea level), average width (Width; in metres), total length encompassed in electrofishing surveys (Length; in kilometres), salmonid species (Salmonid; bnt, brown trout (*Salmo trutta*); bkt, brook trout (*Salvelinus fontinalis*)), estimated density of brown and brook trout (Densily; individuals·$(100m^2)^{-1}$) with upper and lower limit of confidence interval (Upper, Lower), and other species recorded (Other species).

Stream	Coordinates	Altitude	Width	Length	Salmonid	Density	Lower	Upper	Other species
Färsån	63°13′N, 16°06′E	340–380	2.26	2.6	Bnt. 0+	15.0	12.9	17.0	
					Bnt. > 0+	27.1	26.1	28.1	
					Bkt. 0+	1.4	1.4	1.5	
					Bkt. > 0+	11.4	10.5	12.2	
Gulån[a]	63°18′N, 15°52′E	225–280	2.25	4.7	Bnt. 0+	12.1	—	—	Burbot
					Bnt. > 0+	23.2	—	—	
					Bkt. 0+	9.2	—	—	
					Bkt. > 0+	45.0	—	—	
Höglundabäcken	63°08′N, 15°51′E	225–290	2.35	4	Bnt. 0+,	47.8	44.7	50.8	Eurasian minnow
					Bnt. > 0+	24.3	23.6	24.9	
					Bkt. 0+	19.5	18.6	20.4	
					Bkt. > 0+	14.0	13.8	14.2	
Sågbäcken	62°42′N, 14°21′E	385–415	3.06	5	Bnt. 0+,	5.8	5.0	6.7	Burbot, Eurasian minnow
					Bnt. > 0+	4.7	4.1	4.4	
					Bkt. 0+	11.6	11.1	12.1	
					Bkt. > 0+	2.5	2.4	2.7	
Krokdalsbäcken[b]	63°12′N, 15°46′E	270–300	1.82	1.1	Bnt. 0+	29.2	—	—	
					Bnt. > 0+	45.0	—	—	
Slandromsån	63°07′N, 14°38′E	350–405	2.56	1.2	Bnt. 0+	29.0	27.6	30.5	Northern pike
					Bnt. > 0+	50.9	50.3	51.6	
Stugubäcken	63°08′N, 15°34′E	280–325	3.24	3.5	Bnt. 0+	12.3	11.2	13.3	Eurasian minnow, European brook lamprey, bullhead
					Bnt. > 0+	21.0	20.0	22.0	
Bjuråsbäcken[c]	63°03′N, 15°72′E	329–410	2.6	3.1	Bnt. 0+				
					Bnt. > 0+	15.1			

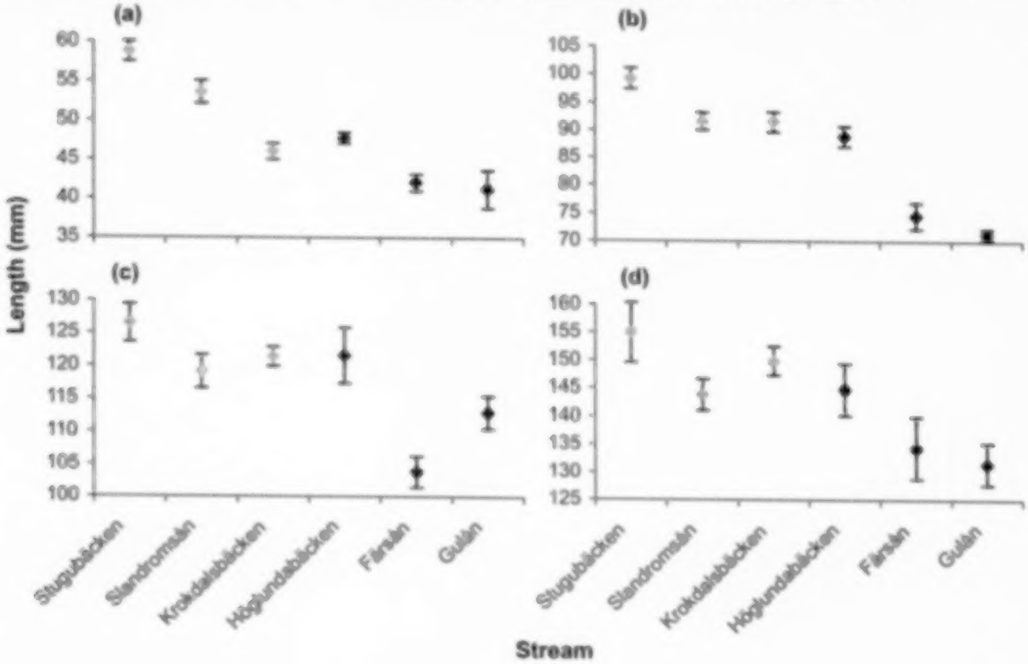
Note: Altitude represents the altitudinal span of sampled reaches within each stream. Other species: burbot, *Lota lota*; Eurasian minnow, *Phoxinus phoxinus*; northern pike, *Esox lucius*; European brook lamprey, *Lampetra planeri*; bullhead, *Cottus gobio*.

[a] Density estimates from Eriksson and Nyberg 2001.

[b] Density estimates from Nordwall et al. 2001.

[c] Density estimates from Näslund et al. 1998.

Fig. 1. Age-specific lengths of brown trout (*Salmo trutta*) (shaded diamonds, allopatric populations; solid diamonds, sympatric populations) in six studied populations with 95% confidence intervals for age classes (*a*) 0+, (*b*) 1+, (*c*) 2+, and (*d*) 3+.



spectively, for each locality. Stream width, average and maximum depth, dominating substrate, and water velocity are measured in the field. The proportion of lakes in the upstream watershed is classified into four area classes: <1%, 1%–5%, 5.1%–10%, >10%. The size of the upstream watershed was also classified from maps: <10 km^2, 10–100 km^2, >100 km^2. The date of fishing was expressed as Julian date (ranging from 1 to 366). The entire database was used for one comparison of the stream size related relative occurrence of brown trout and brook trout.

For comparisons of densities, a subset of data was selected. In SERS, brook trout were present on 520 localities. From these sites, 500 were randomly selected. For each of these 500 localities, the nearest brown trout locality without brook trout was chosen as reference. Each brown trout locality was always in the same watershed size class (<10, 10–100, >100 km^2) and basin as the corresponding brook trout locality and was not allowed to deviate by more than 50 m in altitude from it. Localities used in the analysis ranged from the counties Skåne to Västerbotten (hence distributed over roughly two-thirds of Sweden's surface area) and were located in the altitudinal range of 1–648 m a.s.l. When data from several fishing occasions were available, the latest occasion was chosen. Brown trout localities did not deviate in altitude from brook trout localities (t test, t = 0.073, p > 0.05; mean values of 305 and 300 m a.s.l. for brown and brook trout, respectively). Given the methodology of selecting reference localities, there was no difference in geographical average position (longitude and latitude, i.e., x and y coordinates) or watershed size. In analyses, data were pooled in four classes: brook trout present (n = 500), allopatric brook trout (n = 165), allopatric brown trout (n = 500), and both species present (n = 335).

Estimated densities of fish (expressed as individuals per 100 m^2) were transformed ($\log_{10}$(denstity + 1)) before statistical computations. Comparisons among groups were carried out with one-way ANOVA or ANCOVA when a linear response of dependent variables was present. Homogeneity of variances was tested with the Levenes test. In the analysis, comparisons were pursued using hierarchical linear model approach (e.g., Wagner et al. 2006) and covariates were entered first.

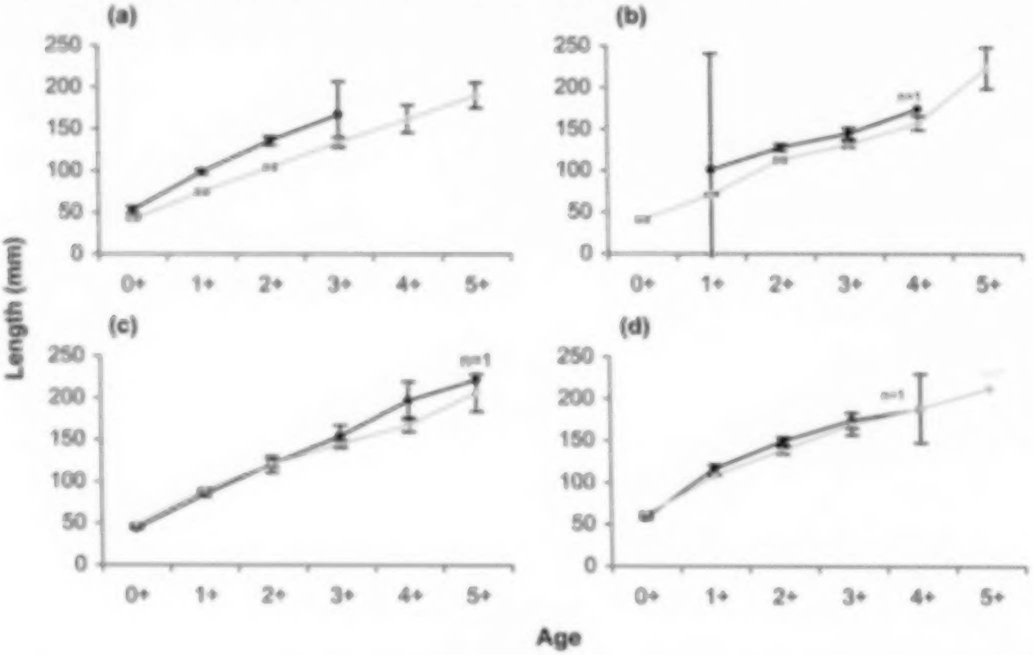
Results

Growth

In the streams of the field study, age-specific lengths were generally longer in allopatric populations of brown trout than in sympatric ones (ANOVA, $F_{[1,16]}$ = 19.93, p < 0.001) (Fig. 1). For each respective age class, brown trout of ages 0+ to 3+ were significantly smaller (ANOVA, Tukey–Kramer's honestly significant difference (HSD) test, mean squared error (MSE) = 41.98, df = 16, mean pairwise difference < 18.6, p < 0.05) in Färsån and Gulån (the sympatric streams in which the two species were most evenly distributed) than in all three allopatric populations, with the exceptions of age class 2+ in Gulån and age class 3+ in Färsån.

Although age in many cases is not determined, SERS provides information on the length of age-0+ fish based on length–frequency distributions. These data confirmed the pattern of the field study as average length of age-0+ brown trout was longer in allopatric populations than in sympatric

Fig. 2. Growth curves for brook trout (*Salvelinus fontinalis*) (solid lines and solid circles) and brown trout (*Salmo trutta*) (shaded lines and shaded diamonds) in (*a*) Färsån, (*b*) Gulån, (*c*) Höglundabäcken, and (*d*) Sågbäcken.



ones. This was not an effect of differences in localities with respect to latitude, season (i.e Julian date), or the abundance of salmonids as these three variables were used as covariates (ANCOVA, $F_{[4,447]} = 45.7$, $p < 0.001$, $r^2 = 0.29$, Levenes $p = 0.21$). Size of catchment (classified) and width of stream were not significantly correlated to size of age-0+ brown trout in this analysis. However, when the effect of water temperature at the sampling occasion was also included as covariate, the effect of brook trout was not significant (ANCOVA, $F = 2.11$, $p = 0.12$). When compensating for the covariates, the size of age-0+ brown trout at Julian date 237 was 57.2 mm (95% confidence interval (CI), 55.9–58.5) without brook trout and 53.2 mm (95% CI, 52.0–54.4) with brook trout present. A similar analysis revealed no significant effects on age-0+ brook trout growth from the presence of brown trout (ANCOVA, $F_{[4,190]} = 20.1$, $p < 0.001$, $r^2 = 0.35$, Levenes $p = 0.30$; significant covariates latitude, Julian date, abundance of salmonids; presence of trout $p = 0.95$).

In the streams of our field study, brook trout grew faster than brown trout (ANOVA, $F_{[1,24]} = 87.91$, $p < 0.0001$). In Färsån and Gulån, the mean length of brook trout was longer for all age classes (Fig. 2). In Sågbäcken, brook trout tended to have a slightly longer average length in most age classes, but this pattern was not as clear as in the earlier-mentioned streams. In Höglundabäcken, brook trout tended to have a higher adult growth rate, whereas juvenile growth rate was similar or perhaps slightly higher for brown trout. The SERS data provided support for the above findings of high brook trout growth rates. Throughout the season from July to October, age-0+ brook trout were generally longer than age-0+ brown trout. Compared at Julian date 238, the average length differed 5.8 mm (brown trout, 55.6 mm; brook trout, 61.4 mm; ANCOVA with species as fixed factor and Julian date as covariate, $n = 589$, $F_{[2,646]} = 94.7$, $p < 0.001$, $r^2 = 0.28$, Levenes $p = 0.538$).

Maturation

The mature brown trout females from sympatric populations were generally older than the ones living in allopatry (ANOVA, $F_{[1,119]} = 6.26$, $p = 0.014$, mean age = 4.1 and 3.7 years for sympatric and allopatric populations, respectively). Estimates were also made for female age at 50% maturity (MA 50). For all three sympatric brown trout populations, these estimates were higher than in two of the allopatric ones, Slandromsån and Stugubäcken (Table 2). The estimate for the third allopatric population in Krokdalsbäcken was not consistent with this pattern, as it was higher than the ones for Gulån and Färsån.

This difference was, however, not significant, and the mature females caught in Krokdalsbäcken were younger than those caught in Färsån (two-sample *t* test, $t = -3.99$, $p < 0.001$, df = 22) and Gulån (two-sample *t* test, $t = -2.33$, $p < 0.05$, df = 22). Confidence limits could not be calculated for Stugubäcken, whereas Slandromsån significantly deviated from all three sympatric populations.

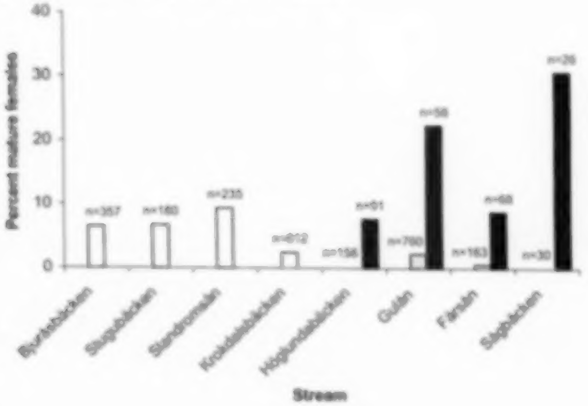
The frequency with which mature females were caught was compared between localities where standardized electrofishing was performed in each stream respectively. Mature brown trout females were more common in allopatry than in sympatry when normalized against the total catch of individuals above age-0+ (Fig. 3) (*t* test, arcsin-transformed data, $t = 2.99$, $n = 4$, $p = 0.03$, df = 5). Comparing the age of the

Table 2. Estimated age at which 50% of females have matured (MA 50), with lower and upper limits of 95% confidence intervals (CIs).

Sympatry or allopatry	Stream	Species	Estimated MA 50	95% CIs Lower limit	95% CIs Upper limit	*N*
Allopatry	Krokdalsbäcken	Brown trout	3.95	3.47	6.74	51 (10)
	Slandromsån	Brown trout	2.93	2.72	3.15	174 (43)
	Stugubäcken	Brown trout	2.98	—	—	113 (20)
Sympatry	Färsån	Brown trout	3.57	3.18	3.91	121 (20)
	Färsån	Brook trout	1.94	—	—	42 (13)
	Gulån	Brown trout	3.7	3.36	4.33	48 (15)
	Gulån	Brook trout	1.71	—	—	31 (27)
	Höglundabäcken	Brown trout	4.09	3.63	4.96	145 (18)
	Höglundabäcken	Brook trout	2.19	1.87	2.54	85 (27)

Note: Brown trout, *Salmo trutta*; brook trout, *Salvelinus fontinalis*. Numbers in parentheses under *N* represent mature females.

Fig. 3. Number of mature females of allopatric and sympatric brown trout (*Salmo trutta*) (open and shaded bars, respectively) and brook trout (*Salvelinus fontinalis*) (solid bars) caught as proportion of all over-yearling individuals.

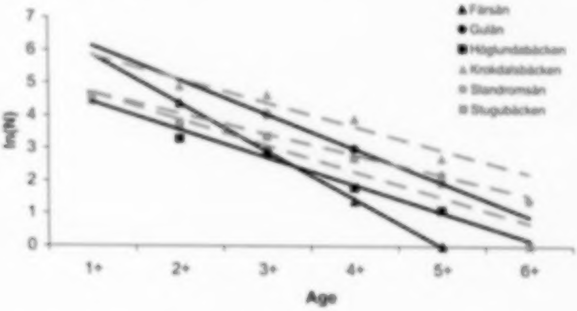


mature females caught revealed that mature brook trout females were significantly younger than brown trout females in Färsån (Wilcoxon test, $W = 0.5$, $p < 0.000001$), Gulån (Wilcoxon test, $W = 42$, $p < 0.00001$), and Höglundabäcken (two-sample *t* test, $t = -2.56$, $p < 0.05$, df = 28). Estimates of female age at MA 50 were lower for brook trout than for brown trout in all three cases (Table 2). Because of small brook trout sample sizes, confidence intervals were only estimated for Höglundabäcken, where brook trout females matured significantly earlier than all three brown trout populations. Mature brook trout females were smaller than mature brown trout females in Färsån and Gulån (ANOVA, log-transformed data, $p < 0.05$). In Höglundabäcken, sizes of mature females were not significantly different. Mature brook trout females were more frequently caught than mature brown trout females when normalized against the total catch of individuals above age-0+ (*t* test, arcsin-transformed data, $n = 3$, $p = 0.024$) (Fig. 3).

Mortality

Sympatric brown trout appeared to have higher mortality rates than brown trout from allopatric populations (ANCOVA, comparisons of slopes, $F_{[1,25]} = 4.46$, $p < 0.05$) (Fig. 4) as estimates were higher for all three sympatric populations compared with all three allopatric ones.

Fig. 4. Catch curves with slopes representing instantaneous mortality rates for six brown trout (*Salmo trutta*) populations. Regression lines indicate sympatry (solid lines) and allopatry (shaded broken lines).



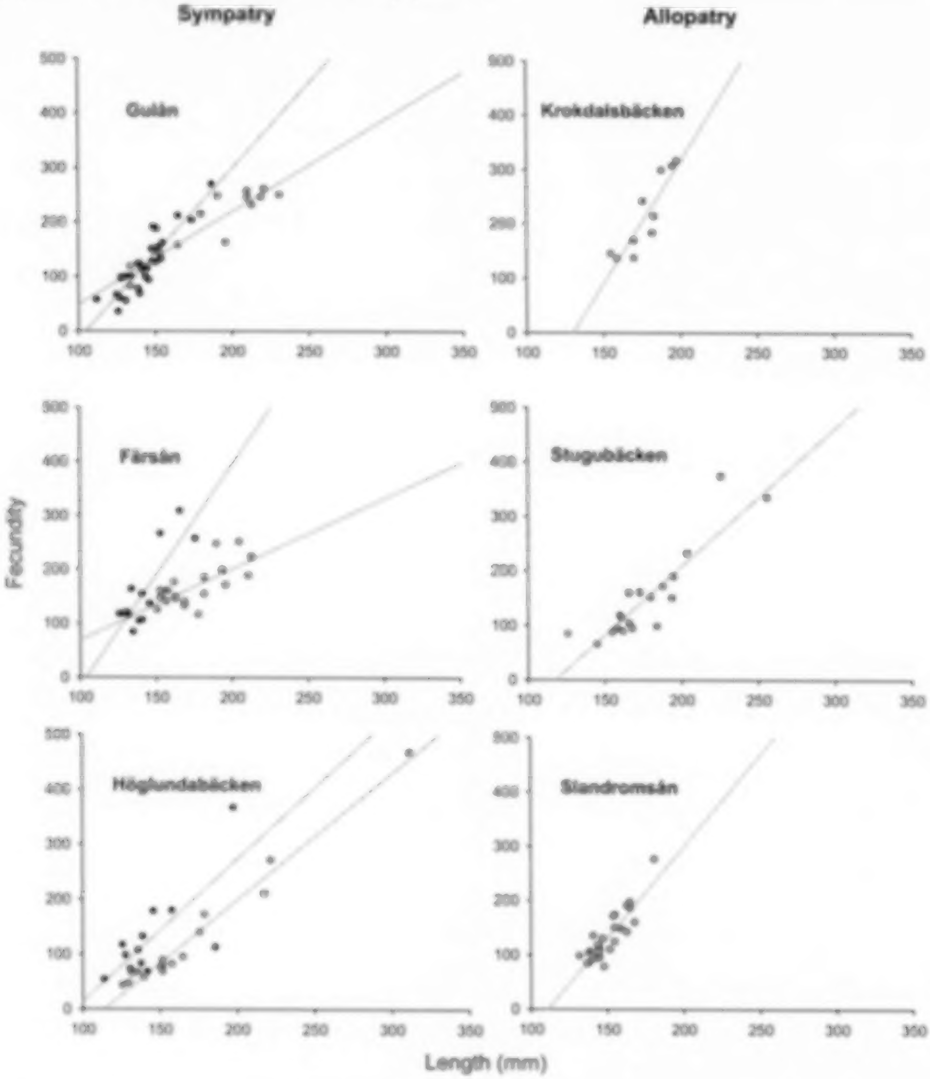
Fecundity

Length-specific fecundity tended to increase faster with length in two of the allopatric populations, Krokdalsbäcken and Slandromsån (Fig. 5). However, when pooled in two groups, there was no difference in length-related rate of increase in fecundity between allopatric and sympatric populations (ANCOVA, log-transformed data, $p = 0.49$). Brook trout females had a higher length-related rate of increase of fecundity than brown trout females in Färsån and Gulån (ANCOVA, log-transformed data, $p < 0.005$) (Fig. 5). In Höglundabäcken, this rate of increase did not differ between females of the two species, but brook trout fecundity was on average higher than that of brown trout (ANCOVA, log-transformed data, $p = 0.0005$).

Spatial and numerical patterns of brown and brook trout distribution

The abundance of brook trout was significantly lower in the presence of brown trout in the SERS data (Table 3). Abundance was $26.8 \cdot (100\ \text{m}^2)^{-1}$ (standard error (SE) = 2.5) in the absence of brown trout and 12.4 (SE 2.8) with brown trout present (Table 3). In a more detailed analysis, using general linear model (GLM) univariate ANCOVA, the effect of brown trout presence on the abundance of brook trout

Fig. 5. Length-specific fecundity in three sympatric brook trout (*Salvelinus fontinalis*; solid circles) and brown trout (*Salmo trutta*; shaded circles) populations and three allopatric brown trout populations.



($\log_{10}(x + 1)$ transformed) was tested using catchment area class and altitude as significant covariates. Brook trout density was negatively affected by the presence of brown trout when the effect of altitude and catchment size was compensated for (ANCOVA, $F_{[1,496]} = 481$, $r^2 = 0.795$, Levenes $p = 0.099$, $p < 0.001$). A corresponding analysis of the effect of brook trout presence on the abundance of brown trout could not be done because of unequal variances when altitude and catchment size was compensated for (ANCOVA, Levenes $p < 0.001$). Densities of brown trout did not, however, differ based on the presence or absence of brook trout (Table 3), and this pattern was consistent in both small (catchment areas < 10 km^2, ANOVA, $F = 0.994$, $p > 0.05$) and large (catchment areas > 10 km^2, ANOVA, $F = 0.445$, $p > 0.05$) streams.

In one-species systems, densities of brown trout (average = 22.6 individuals·(100 m^2)$^{-1}$, SE = 1.7) did not differ significantly from those of brook trout (average = 26.8 individuals·(100 m^2)$^{-1}$, SE = 2.5). The combined sympatric abundances of brook trout and brown trout (32.8 individuals·(100 m^2)$^{-1}$, SE = 3.6) were significantly higher than allopatric densities at sites where brown trout lived alone (ANOVA, $F = 23.6$, $p < 0.001$) but not at sites where brook trout was the only species present (ANOVA, $F = 2.28$, $p = 0.13$). Of sympatrical populations, the majority were numerically dominated by brown trout (Table 4), a pattern that did not seem to be affected by watershed size (χ^2, df = 2, $p > 0.05$). On the other hand, the proportion of populations that were allopatric was affected by watershed size and differed significantly between brook and brown

Table 3. Average abundance (± standard error) of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in allopatry and sympatry.

	Brook trout	Brown trout	*F*	*p*	*N*
Allopatry	26.8 (2.5)	22.6 (1.7)	1.982	0.156	165; 500
Sympatry	12.4 (2.8	20.4 (1.9)	71.7	**<0.001**	335; 335
F	90.3	1.06			
p	**<0.001**	0.305			
N	165; 335	500; 335			

Note: Differences between groups tested with one-way analysis of variance. Bold type indicates significant effects. In the *N* column, the two numbers in each field refer to the number of sampled sites with brook and brown trout, respectively. In the *N* row, the two numbers refer to the number of allopatric and sympatric sites, respectively.

Table 4. Proportion (%) among watershed sizes of (*a*) sympatric SERS sites numerically dominated by brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) and (*b*) SERS sites at which brown trout and brook trout populations are allopatric or sympatric.

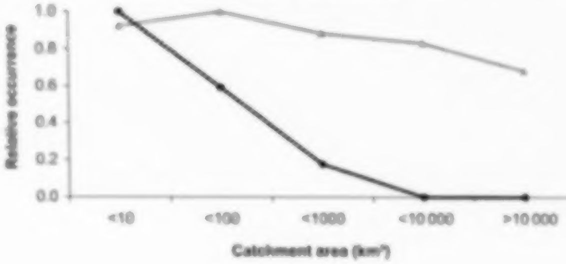
		Catchment area (km^2)			
		<10	10–100	>100	Total
(*a*) Sympatric SERS sites					
Brown trout	Sympatry	64.2	74.9	68.2	70.5
Brook trout	Sympatry	35.8	25.1	31.8	29.5
N		123	191	21	335
(*b*) Allopatric or sympatric SERS sites					
Brown trout	Allopatry	63.3	57.7	54.2	59.9
	Sympatry	36.7	42.3	45.8	40.1
N		335	452	48	835
Brook trout	Allopatry	47.7	19.7	21.4	33
	Sympatry	52.3	80.3	78.6	67
N		235	238	27	500

trout (χ^2, df = 2, $p < 0.001$). Brook trout had a more pronounced concentration of allopatric populations in the smallest watersheds (Table 4).

The frequency with which brook trout has been encountered on electrofishing occasions within the SERS data was negatively correlated to catchment area size (Pearson $r = -0.94$, $p = 0.016$) (Fig. 6). Brook trout was found on 4.9% of fishing occasions in streams of the smallest catchment size class, a percentage that declined as catchment size increased. Frequency of brown trout occurrence also seemed to have a weak negative correlation with catchment size. This correlation was, however, not significant (Pearson $r = -0.862$, $p = 0.06$), and brown trout was less common in catchments smaller than 10 km^2 than in catchments between 10 km^2 and 100 km^2.

Although brook trout and allopatric brown trout localities did not differ in date of sampling, altitude, or geographical position, brook trout localities were on average lower in water temperature (10.7 °C (SE 0.4 °C) for brook trout vs. 11.8 °C (SE 0.2 °C) for brown trout; ANOVA, $F = 5.8$, $p = 0.017$), which could indicate a higher degree of groundwater influx. An increase in the proportion of groundwater should lead to a decrease in the relative importance of air temperature in determining water temperature. To test this, correlations between air and water temperatures on brook and brown trout localities were compared. Water temperature on brook trout localities showed a lower degree of correlation to air temperature (ANCOVA, species as fixed factor and air temperature as covariate, $p < 0.001$, $n = 478$, $r^2 = 0.64$). After compensating for differences in air temperature, brook trout streams were exactly 1.0 °C colder than allopatric brown trout streams (at a given day during late July to mid-September).

Fig. 6. Relative proportion of electrofishing occasions (n = 32 448) when brook trout (*Salvelinus fontinalis*; solid line and solid circles) and brown trout (*Salmo trutta*; shaded line and shaded triangles) were present. Percentage of occasions when the species was found in each catchment size class has been divided with the maximum percentage of occurrence.



Discussion

By using large amounts of electrofishing data in SERS, we were able to detect clear effects of interspecific competition between brown and brook trout in Swedish streams. SERS data demonstrated a pattern in which interactions between the two species generally were asymmetrically in favour of brown trout at a majority of sympatric sites. Brook trout densities were negatively affected by brown trout presence, whereas brown trout densities seemed unaffected by brook trout in both small and larger streams. Furthermore, sympatric brown trout densities were higher than those of brook trout, and the majority of sympatric localities were numerically dominated by brown trout also in the smallest watershed class. Analyses of SERS data thus failed to show the change in competitive asymmetry with stream size that is expected if condition-specific competition is causing the species replacement patterns we observe in nature.

Brown trout had lower growth rates in coexistence with brook trout, a pattern that was consistent also in our field-study streams. The effect of brook trout in reducing brown trout growth in the SERS data did, however, seem quite weak (not significant), and lowered growth rates were to a large extent caused by environmental factors, e.g., low water temperatures linked to brook trout presence. This link between successful brook trout invasions and habitat-related limitations on brown trout growth rates, together with the asymmetrical competitive effects on densities, suggest that brown trout performance is an important factor in structuring the outcome of Swedish brook trout introductions.

Although the competitive asymmetry seemed continuous throughout the size span of sympatric sites, a contradictive pattern was to some extent demonstrated by the fact that the frequency of brook trout one-species systems increased in the smallest streams. Obviously, this could be explained partially by the possibility that brook trout have become established in streams where brown trout were missing in the first place. However, brown trout should have had access to most allopatric brook trout localities as it is a very common species with better swimming ability than brook trout (Peake et al. 1997). Therefore, the more logical explanation is that brown trout are often unable to sustain viable populations where brook trout are numerically dominant. As there seems to be no continuous shift in competitive ability along a stream size gradient, it thus seems that negative effects of brook trout on brown trout quickly change from low to detrimental as regards the ability of brown trout to sustain a viable population. Consequently, localities in which brook trout are highly dominant are likely to be excluded from our analysis of growth and densities in sympatry simply because they have become one-species systems over time.

We found that Swedish brook trout populations are found mostly in small, cold streams, a pattern that agrees well with findings in North American brook trout – brown trout systems. These habitats generally provide lower growth potential for stream-resident fish than larger streams, as demonstrated in the SERS data by lowered brown trout growth rates. Although temperature preferences, optimal temperature for growth, and ability to withstand high and low temperatures appear quite equal (MacCrimmon and Campbell 1969; Raleigh 1982; Elliot 1994), brook trout seem to gain from low temperatures when competing with brown trout. Even if brook trout growth rates are equally lowered, the life history of brook trout could give a competitive advantage in cold streams. In accordance with North American literature, we found brook trout populations having higher juvenile growth rates and earlier reproduction compared with those of brown trout. In combination with higher length-specific fecundity and higher proportions mature females, this potentially gives brook trout a substantially higher population growth rate, suggesting an adaptation to habitats with a low potential for adult growth and maturation.

Stream-resident brown trout use different parts of a stream during ontogeny: juveniles dwell in shallow gravelly rapids, whereas larger individuals often migrate to deeper areas like pools and backwaters (Bohlin 1977; Näslund et al. 1998). Studies on large-scale migration (from stream to larger stream, lake, or sea) have emphasized the particular importance of such strategies for females, as their fecundity is directly dependent on body size (Jonsson 1985). However, the same principles also seem to apply for small-scale within-stream habitat shifts as females need to reach a larger size than males before first maturation (Näslund et al. 1998). Näslund et al. (1998) suggested that brown trout females in a low-productive small stream should depend heavily on habitat shifts to be able to reach the minimum size of maturity. As a consequence, population fecundity will be very dependent on physically large habitats like deep pools and beaver ponds. Such habitats are often in short supply in small streams, a fact that could cause entire populations of stream-resident brown trout to rely on a very small number of females spawning each year. If conditions for growth become so poor that female maturation and thereby population fecundity become limiting for population growth rates, brook trout will undoubtedly be able to sustain viable populations beyond the point at which brown trout population fecundity is too low to maintain a stable population size. Interestingly enough, the numbers of mature brown trout females were strikingly low in the streams of our field study. This was particularly prominent in the sympatric populations in which mature brook trout females were more frequent, less congregated, and found in a larger variety of habitats than those of brown trout. Somewhere down a stream-size gradient, any given combination of low resource levels, low water temperatures, and physically constrained habitats could through reduced individual growth rates make population fecundity a limiting factor for brown trout population growth rates. Higher growth rates, as well as demographic advantages, should enable brook trout to maintain populations well beyond this point, as indicated by a recent study in which brook trout populations were found in extremely small Swedish streams with mean annual discharge as low as 2.5 $L \cdot s^{-1}$ (M. Lindberg, Swedish University of Agricultural Sciences, Department of Aquaculture, SE-901 83 Umeå, Sweden, personal communication, 2006).

Obviously, our field-study sites constitute "snapshots" in the continuous environmental gradient over which species-specific changes in fitness occur. Mechanistic modelling work and better measurements of how life history parameters and physiological rates change from brown trout streams to brook trout headwaters are essential parts in a future development of a thorough understanding of the dynamics of these systems. However, our analyses of life history characteristics has given new and valuable information about the different strategies of the two species and how the life history of brown trout can differ between sites where brook trout has or has not invaded. When it comes to generality, our use of large amounts of electofishing data has enabled a rather unique possibility of describing competitive patterns on a large geographical scale. Our approach does not allow us to definitely reject or support condition-specific competition as the responsible mechanism behind species replacement patterns in Swedish brown trout – brook trout systems; however, it has added to a growing amount of evidence (e.g., McHugh and Budy 2005) that species replacement patterns along altitudinal gradients could be the result of different dynamics structuring up- and down-stream distributions of interacting species. We found no or weak competitive effects of brook trout presence on brown trout performance on sympatric sites, whereas coexistence of the two species was linked to an at least partially habitat-related reduction of brown trout growth rates. Hence, we see no evidence for a gradually increasing competitive ability of brook trout. Furthermore, our field-study results indicate that reduced growth rates in habitats in which brook trout are able to invade are accompanied by lower numbers of mature brown trout females. If this mechanism is responsible for limiting the production of otherwise competitive brown trout, we would expect a "threshold value" of growth potential at which brown trout cohort size would become limiting for brown trout production and ability to endure competition from brook trout. From this theoretical point on, brown trout would not be able to compensate for the higher reproductive potential of brook trout. Intriguingly enough, we see an increase in the frequency of allopatric brook trout populations in the smallest streams. This is not correlated with an increased competitive ability in small sympatric systems, indeed suggesting an "all or nothing" effect of brook trout competition. Although SERS data gave weak evidence for effects of brook trout presence on brown trout performance, examples of Swedish brown trout populations being replaced by brook trout are not uncommon (Spens et al. 2007). Our results suggest as a plausible hypothesis that this generally happens in systems in which brown trout recruitment is severely limited. We suggest that population fecundity rather than individual interference or exploitation competitive ability per se could be a critical factor limiting competitive abilities and distribution of brown trout in Swedish brook trout dominated headwaters.

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Variation in lake sturgeon (*Acipenser fulvescens*) abundance and growth among river reaches in a large regulated river

Tim J. Haxton and C. Scott Findlay

Abstract: Lake sturgeon (*Acipenser fulvescens*) stocks are well below historical levels across their natural range. In this study, we examine why lake sturgeon have not substantially recovered to historical levels in a large regulated river (Ottawa River, Canada). Three primary anthropogenic stressors have been identified as potentially limiting lake sturgeon populations in the Ottawa River: (*i*) commercial harvest, (*ii*) contaminants, and (*iii*) water power management. Hypotheses *i* and *iii* were tested by comparing lake sturgeon abundance and examining growth among reaches differing in level of commercial harvest and water management regime; hypothesis *ii* was tested by assessing contaminant loads in lake sturgeon and examining effects on growth and condition. Relative abundance, growth, mortality, and mean size of lake sturgeon did not differ among river reaches with (n = 6) and without (n = 3) a commercial harvest. Mercury was the only contaminant that was elevated. Neither growth nor condition showed any detectable relationship with mercury body burden. Relative abundance of lake sturgeon was greater in unimpounded than impounded reaches; additionally, there is evidence of faster growth in the impounded versus unimpounded reaches, suggesting density-dependent compensation. Water power management appears to be the primary factor affecting lake sturgeon in this river.

Résumé : Les stocks d'esturgeons jaunes (*Acipenser fulvescens*) ont des densités très inférieures à celles du passé dans toute leur aire de répartition naturelle. Nous cherchons à savoir dans notre étude pourquoi les esturgeons n'ont pas en grande partie retrouvé leurs densités du passé dans une grande rivière à débit contrôlé (l'Outaouais, Canada). Nous avons identifié trois sources anthropiques principales de stress qui limitent potentiellement les populations d'esturgeons jaunes dans l'Outaouais : (*i*) la récolte commerciale, (*ii*) les contaminants et (*iii*) l'aménagement hydro-électrique. Nous avons testé deux des hypothèses *i* et *iii* en comparant l'abondance et la croissance des esturgeons jaunes dans des sections qui diffèrent par l'intensité de la pêche commerciale et le régime de gestion des eaux; nous avons évalué l'hypothèse *ii* en déterminant les charges de contaminants des esturgeons jaunes et en examinant leurs effets sur la croissance et la condition. L'abondance relative, la croissance, la mortalité et la taille moyenne des esturgeons jaunes ne diffèrent pas entre les sections de rivière avec (n = 6) et sans (n = 3) récolte commerciale. Le mercure est le seul contaminant à présenter des valeurs élevées. Ni la croissance, ni la condition ne semblent être reliées de façon décelable à la charge corporelle de mercure. L'abondance relative des esturgeons jaunes est plus importante dans les sections sans barrage que dans celles transformées en réservoirs; de plus, il y a des indications que la croissance est plus rapide dans les réservoirs que dans les sections de rivière non modifiées, ce qui semble indiquer une compensation dépendante de la densité. L'aménagement hydro-électrique paraît être le facteur principal à affecter l'esturgeon jaune dans la rivière.

[Traduit par la Rédaction]

Introduction

Sturgeon are purportedly the most threatened vertebrate group on the planet (Ludwig 2006). Acipenseriformes, comprising 27 extant species (including both sturgeon and two species of paddlefish), are widespread throughout the northern hemisphere, and all species are imperilled (Billard and Lecointre 2001; Pikitch et al. 2005). Potential threats include commercial harvest (Rochard et al. 1990; Birstein 1993; Beamesderfer and Farr 1997), habitat deterioration and loss (Rochard et al. 1990; Birstein 1993; Beamesderfer and Farr 1997), population isolation and habitat fragmentation, especially by dams (Rochard et al. 1990; Birstein 1993; Beamesderfer and Farr 1997), and poaching (i.e., for caviar; Ludwig 2006).

The lake sturgeon (*Acipenser fulvescens*) is endemic to North America and was historically abundant (Harkness and Dymond 1961; Scott and Crossman 1973). However, popula-

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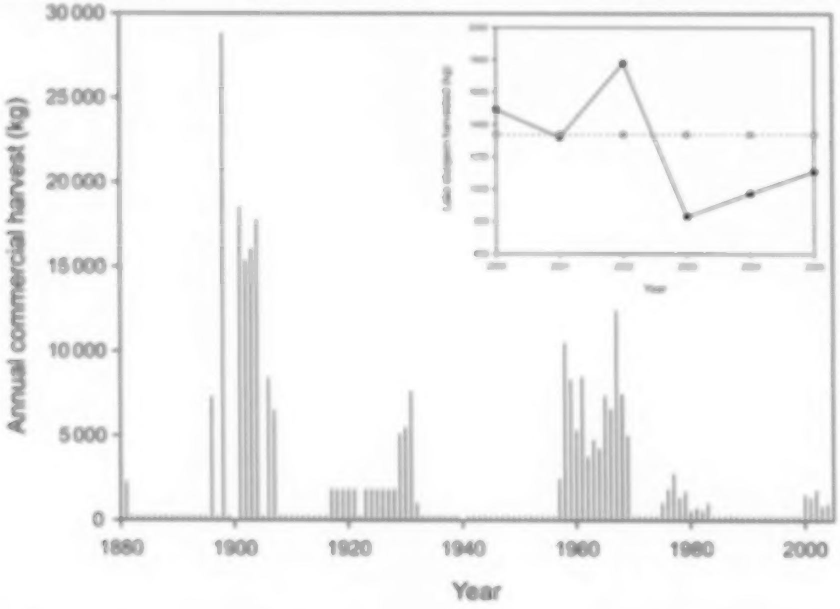


Fig. 1. Reported annual commercial harvest (kg) of lake sturgeon (*Acipenser fulvescens*) from the Ottawa River from 1880–2005. Zero catches represent missing data except for 1956, 1971–1974, 1984–1986, and 1989. For the years 1956–1975, commercial harvests are for both the Ottawa River and southern Ontario inland lakes. During the periods (1964–1974) where harvest data exist for both the Ottawa River and southern Ontario inland lakes, the Ottawa River harvest represented on average 33.5% (±49% standard deviation, SD) of the total harvest. Inset: current commercial harvest of lakes sturgeon from 2000 to 2005; dotted line represents annual quota.

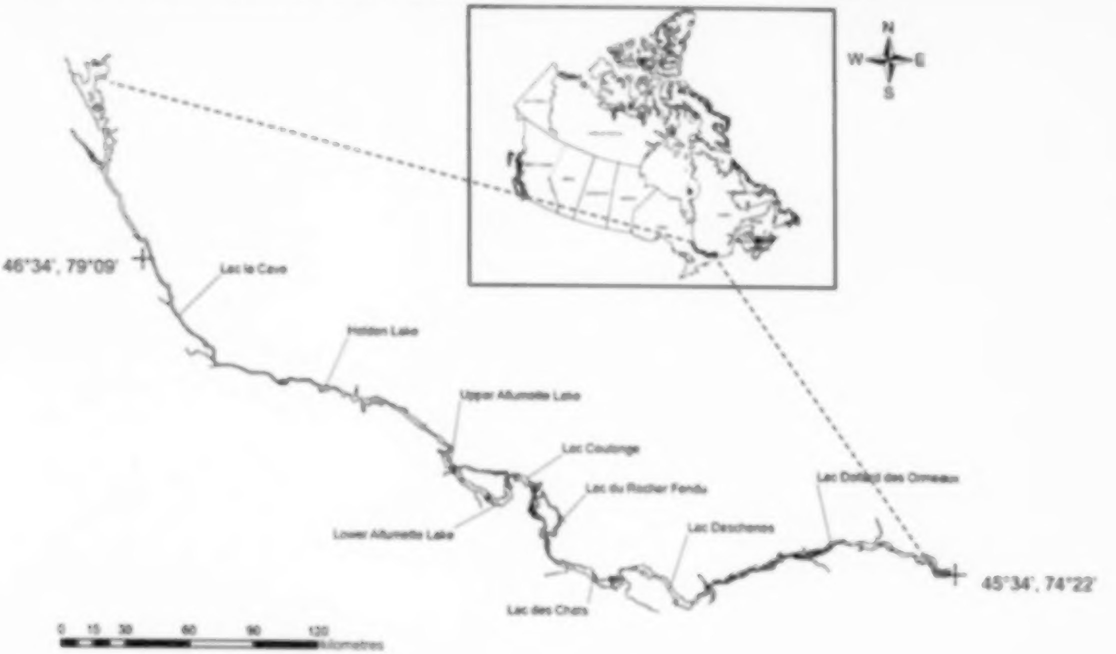
tions have declined precipitously throughout their range and are currently considered at risk in many states and provinces (Williams et al. 1989; Kempinger 1996; Williamson 2003). Sturgeon life history traits, including low recruitment, slow growth, late maturity, and periodic spawning, not only render populations sensitive to increased adult mortality (as occurred, for example, with the large commercial harvests in the late 1800s (Prince 1905; Houston 1987; Holzkamm and McCarthy 1998)), but also have inhibited population recovery (Boreman 1997; Crouse 1999; Gross et al. 2002). Large commercial harvests in many cases were accompanied by deterioration in water quality and loss or degradation of habitat and population isolation by dams constructed for hydroelectric development, flood control, or navigation. Although some of these stresses have been ameliorated, sturgeon populations in general have not recovered to historical levels (Houston 1987; Auer 1996*a*; Baker and Borgeson 1999).

Although at one time considered abundant in the Ottawa River (Small 1883; Dymond 1939), lake sturgeon numbers declined dramatically during the early part of the 20th century (Toner 1943). A commercial lake sturgeon fishery, established in 1881, peaked at a harvest of 28 780 kg in 1898 (Dymond 1939) and declined thereafter. Although a commercial fishery still exists in portions of the Ottawa River, sturgeon harvest is currently at least an order of magnitude smaller than at the turn of the century (Fig. 1). A reduction in sturgeon harvest across Ontario was attributed to stressed (overexploited) populations — less than one-third of the quotas issued across Ontario were filled in 1984. This reduced harvest was driven by abundance as opposed to market forces (Brousseau 1987).

The first part of the 20th century until the early 1970s also saw a dramatic reduction in water quality in the Ottawa River associated with adjacent land use practices (primarily agriculture and forestry), untreated municipal sewage discharge, use of the river for garbage disposal (Ontario Water Resources Commission and Quebec Water Board 1971), the presence of massive log drives, which exceeded one million cords in the late 1800s to early 1900s (Ottawa River Engineering Board 1965), and the construction of a number of pulp mills with untreated discharge (Ontario Water Resources Commission and Quebec Water Board 1971). Dams were constructed along the river and in major tributaries between the 1880s and 1964 (Ottawa River Engineering Board 1965), altering habitat and potentially isolating and fragmenting lake sturgeon populations.

Since the 1970s, the river has experienced changes that might be expected to reduce stress on lake sturgeon populations. All discharge from pulp and paper mills, as well as all municipal sewage, receives primary if not secondary or tertiary treatment. Moreover, more than 90% of municipal sewage is subjected to phosphorus removal (Environment Canada, Environnement Québec, and Environment Ontario 1989). Log drives on the Ottawa River ceased in 1990 and therefore no longer litter the river bottom with sunken logs and wood debris. Commercial harvest for lake sturgeon has all but ceased; all commercial licenses on the Ontario portion of the river were bought out in the late 1980s, and the Quebec portion has had only two licensees since the early 1990s with quotas set at 0.1 $kg \cdot ha^{-1}$ (Henri Fournier, Ministère des Ressources naturelles et de la faune du Qué-

Fig. 2. Ottawa River reaches included in the study. Insert: location of study site in relationship to Canada.



bec, 98 rue Lois, Gatineau, QC J8Y 3R7, personal communication).

Yet, variation in the relative abundance of lake sturgeon was observed among river reaches (Haxton 2002), suggesting that recovery has not occurred in all river reaches, if indeed significant recovery has occurred at all. At least three (not mutually exclusive) hypotheses can be advanced to explain the lack of recovery: (*i*) that although commercial harvesting has declined dramatically, given historical declines and sturgeon life history, it is still sufficiently high to prevent population recovery; (*ii*) population recovery is hampered by high contaminant levels and their attendant impacts on growth and reproduction; and (*iii*) the possibility of population recovery to anything approaching historical levels is effectively precluded by the current water management regime on the river. We investigate these hypotheses by assessing the relationship between lake sturgeon growth, condition, and relative abundance in different reaches of the Ottawa River that vary in their levels of three anthropogenic stressors: commercial harvest, contaminants, and water power management.

Materials and methods

Study site

This study was conducted in nine reaches of the Ottawa River, Canada (Fig. 2). The Ottawa River is a large, highly altered, managed system. The full course of the river extends 1130 km from the headwaters at Lake Capitmitchigama in Québec to the confluence at the St. Lawrence River (Legget 1975), forming a natural provincial border between Ontario and Québec for approximately 580 km from Lake Temiscaming to Carillon (Chapman and Putnam 1984). The river has a watershed of over 146 000 km^2 (65% within Quebec), a mean annual flow of 1968 m$^3 \cdot$s^{-1}, and a vertical descent of 365 m (Telmer 1996), making it ideal for hydroelectric production. This study is restricted to the nine reaches identified in Fig. 2. Reaches are delineated by the presence of dams or sets of rapids. Six of the nine river reaches are controlled by dams, although water management regimes (Table 1) and water level fluctuations vary among these reaches (Fig. 3). Water flows, obtained from several locations along the river, increase from upstream to downstream but show similar patterns that follow a natural flow regime, with the greatest flows occurring in spring and the lowest flows occurring during the summer months and then increasing again during the fall. Water flows were not substantially altered after the construction of Chats Generating Station (G.S.) in 1932 but changed dramatically after the construction of Chenaux G.S., Rolphton G.S., and Otto Holden G.S. (Table 1), with a 42% increase in flows during the winter months and a 25% decrease in peak flows during the freshet.

To examine the potential effects of impoundment on lake sturgeon recovery, reaches were classified as either unimpounded or impounded. Unimpounded reaches (Upper Allumette Lake, Lower Allumette Lake, and Lac Coulonge) are those without dams (Table 1). Riparian areas were not flooded or altered as a result of dam construction, and natural rapids exist (e.g., Allumette Rapids). By contrast, impounded reaches (Lac Dollard des Ormeaux, Lac Deschênes, Lac des Chats, Lac du Rocher Fendu, Holden Lake, and Lac la Cave) are those with dams, where extensive areas have been flooded and dam operations influence water levels and flows directly. If lake sturgeon population recovery is inhib-

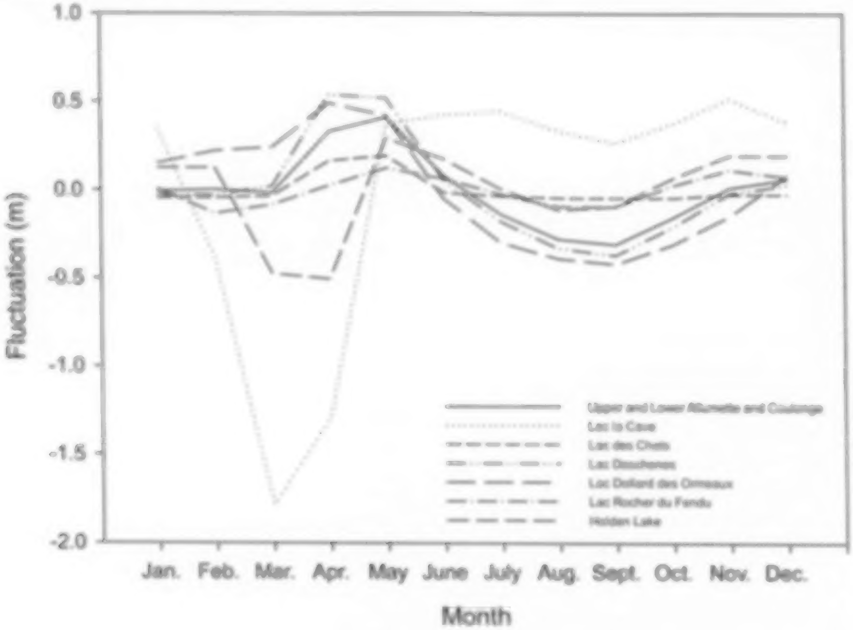
Table 1. Characteristics of Ottawa River reaches including water management regime, water level fluctuation, area flooded as a result

Reach	Length (km)	Surface area (ha)	Mean depth (m)	Natural rapids present	Dam controlled	Year constructed
Lac Dollard des Ormeaux	113.1	14 414	6.1	No	Carillon G.S.	1964
Lac Deschênes	52.8	10 900	5.2	Yes	Chaudière Falls	1880s
Lac des Chats	40.0	7 513	4.9	No	Chats Falls G.S.	1932
Lac du Rocher Fendu	31.1	3 893	7.9	Yes	Chenaux G.S.	1950
Lac Coulonge	18.1	2 888	3.8	Yes	n/a	
Lower Allumette Lake	22.3	4 613	2.9	Yes	n/a	
Upper Allumette Lake	76.9	13 212	10.1	Yes	n/a	
Holden Lake	90.0	7 592	16.8	No	Rolphton G.S.	1950
Lac la Cave	49.0	3 028	19.7	No	Otto Holden G.S.	1952

Note: G.S., generating station; n/a, not available.

*Quebec portion of the river.

Fig. 3. Monthly deviations around the mean annual water level among Ottawa River reaches. Unimpounded reaches (Upper Allumette, Lower Allumette, and Lac Coulonge) are combined.



ited by the current water management regime, then impounded reaches should, on average, show lower abundance and (or) recruitment than unimpounded reaches.

To examine the effects of commercial harvest on lake sturgeon recovery, river reaches were classified as either having a commercial harvest for lake sturgeon (Lac Deschênes, Lac des Chats, Lac du Rocher Fendu, Lac Coulonge, Lower Allumette Lake, and Upper Allumette) or not (Lac la Cave, Holden Lake, and Lac Dollard des Ormeaux; Table 1). All river reaches supported a commercial harvest at one time. Commercial harvest of lake sturgeon in Lac Dollard des Ormeaux was closed in 1992 as the result of overexploitation and mercury burden (Fortin et al. 1992); Lac la Cave and Holden Lake did not produce any sturgeon in 1987, despite a quota of 800 kg (Fortin et al. 1992), and the commercial fisheries were subsequently closed. If recovery is inhibited by ongoing commercial harvest, then we would expect lower abundance in reaches with a commercial harvest versus those without as a consequence of increased mortality. Moreover, because harvest usually results in removal of large, more commercially valuable individuals (Houston 1987), the average size of lake sturgeon would be expected to be smaller in those reaches with an existing commercial harvest versus those without.

The contaminant exposure hypothesis was evaluated in two ways. First, if contaminants are negatively affecting sturgeon populations, one potential effect may be through reduced growth and (or) condition. This can be evaluated by assessing whether in Ottawa River lake sturgeon, growth and (or) condition decline with increasing contaminant loading. Second, because estimates of body burden are available for other North American lake sturgeon populations, we can as-of dam construction, and commercial fisheries.

Water level fluctuation (m)				
Average	Maximum	Water management	Area flooded (km^2)	Current commercial lake sturgeon fisheries
1.5		Run-of-the-river; peaking (winter)	n/a	n/a
	0.9	Run-of-the-river	n/a	0.1 kg·ha^{-1} [a]
0.34		Run-of-the-river	n/a	0.1 kg·ha^{-1} [a]
1.6		Peaking	7.4	0.1 kg·ha^{-1} [a]
0.72		n/a		0.1 kg·ha^{-1} [a]
0.72		n/a		0.1 kg·ha^{-1} [a]
0.72		n/a		0.1 kg·ha^{-1} [a]
2.3	3.0	Reservoir - winter drawdown	45.6	n/a
3.3	4.1	Reservoir - winter drawdown	13.7	n/a

sess (*i*) whether there is any relationship between Hg burden and population status (e.g., declining, stable, and increasing) and (*ii*) where Hg burden of Ottawa River sturgeon fits in this relationship, if indeed any such relationship exists. Contaminant sample sizes were not sufficient to examine among-reach variation, even when categorized as impounded and unimpounded.

Netting assessment

Nearshore community index netting (NSCIN) and fall walleye index netting (FWIN), netting protocols used by the Ontario Ministry of Natural Resources, were used to sample fish communities. NSCIN used randomly set trapnets from early August through early October (water temperature >13 °C; Stirling 1999). Unbaited trapnets, 1.8 m trapnets with 36.5 m leads, and 2.4 m trapnets with 61.0 m leads (3.8 cm mesh) were used. Water depths were restricted to 1.7–3.5 m for the 1.8 m trapnets and 2.3–4.7 m for the 2.4 m trapnets. The shoreline of each reach was partitioned into 2000 m sections, which were numbered and then randomly chosen. Trapnets were set at random locations perpendicular to the shore at least 500 m apart for a 24-h period. At the end of the sampling period, each net was lifted, all fish were identified, enumerated, measured, weighed, an aging structure obtained from lake sturgeon, and then released. The nets then were reset in another randomly chosen location. Attempts were made to sample each reach with at least 40 net sets. No sampling sites were reused if possible; if not possible, a minimum of 4 days must have lapsed from the previous netting before the sampling site was reused (two sites were reused in this study). One or two reaches were assessed annually by NSCIN from 1998–2004.

FWIN uses randomly set monofilament gillnets in the fall when surface water temperatures are between 10 and 15 °C. Gillnets had eight panels of different (25–152 mm stretched) mesh and were set perpendicular to the shore. Nets were randomly set in two depth strata, 2–5 m and 5–15 m, with each depth stratum sampled equally (Morgan 2002). Sample sites were determined by partitioning the reach into 1 km × 1 km numbered quadrats and randomly selecting a quadrat. Netting effort depends on surface area of the waterbody (Morgan 2002). Nets were fished overnight and picked up early the following day (generally an 18- to 24-h net set). FWIN is a lethal sampling technique for most species, with the exception of lake sturgeon and channel catfish. Nets were then reset in another random location. FWINs were conducted on select reaches each year from 1998–2003. Catch per unit effort (CPUE, number of lake sturgeon caught per net night) was estimated for each site for both NSCIN and FWIN.

To increase sample size, lake sturgeon that were sampled during spawning assessment (Haxton 2006; T.J. Haxton, unpublished data) or outside of standardized index netting projects (T.J. Haxton, unpublished data) were included in our analysis of growth, but not in any other analyses.

Total length and fork length (to the nearest millimetre) and weight (to the nearest 100 grams) were measured for all lake sturgeon. A section (1 cm) of the leading pectoral ray was extracted for aging. Commencing in 2001, a numbered monel tag was attached to the anterior portion of the dorsal fin of each lake sturgeon. All lake sturgeon except those taken for contaminant analysis were live-released. Pectoral rays were dried for at least 30 days and then 60 µm sections were extracted using a Buehler low-speed isomet saw (Buehler Ltd., Lake Bluff, Illinois) (Wilson 1987). Pectoral ray sections were examined under a 25× microscope and annuli were counted. Translucent bands are deposited during summer growth and opaque bands are deposited during winter growth (Noakes et al. 1999). A drop of mineral oil was used to illuminate the zones. Ages were estimated from undamaged pectoral rays. Ages were not validated but were estimated by multiple readers; the final decision on age was assigned by the lead author.

von Bertalanffy's growth curves (Ricker 1975) were constructed for lake sturgeon with parameters determined by a least squares nonlinear regression using Solver in Microsoft Excel (Microsoft Corporation, Redmond, California); constraints were placed on parameters (L_∞, 100 (minimum), 150 (maximum); k, 0.001 (minimum), 1.0 (maximum); t_0, −3 (minimum), 0 (maximum)) to ensure convergence. Age–size data were pooled over reaches within a water management regime or commercial harvest category (e.g., impounded or unharvested) to estimate von Bertalanffy's growth parameters, as sample sizes for individual reaches were often too small to permit sufficiently precise estimates of growth parameters. von Bertalanffy's growth curves were then constructed for lake sturgeon in unimpounded reaches, reaches under water power management, reaches commercially harvested, and reaches without a commercial harvest. Bootstrapped confidence intervals on estimated growth parameters were obtained by sampling with replacement *n* individuals (where *n* is the size of actual sample), estimating growth parameters, and estimating the confidential intervals (CIs) based on the parameter distribution over the 1000 trials.

Catch curves were constructed for each sampling technique to assess gear selectivity (Van den Avyle 1993). Size classes were partitioned into 5 cm (total length) bins and plots were constructed of $\log_{10}$ frequency versus size class. Lake sturgeon were considered fully vulnerable to gear at the mode of the frequency distribution. A *t* test was conducted on the total length of the lake sturgeon caught by different depth strata in the FWIN to determine if they were size selectivity based on gear depth.

Annual mortality was determined from age class frequency distributions, with ages grouped in 5-year intervals. Instantaneous mortality (z) was calculated by regressing the logarithm of age class frequency on age on the descending limb of the catch curve (Ricker 1975). Annual mortality (A) was determined from $A = 1 - e^{-z}$ (Ricker 1975). Bootstrapped confidence intervals on estimated mortality were obtained by sampling with replacement *n* individuals (where *n* is the size of actual sample), estimating mortality, and estimating the CIs based on the mortality estimate distribution over the 1000 trials.

Forty-eight lake sturgeons from five reaches were collected for contaminant analysis. A 500 g sample of epaxial muscle was sent to the Ontario Ministry of Environment for contaminant analysis, specifically organochlorine pesticides, which are widely used in insecticides, polychlorinated biphenyls (PCBs), which have many industrial uses (Ministry of the Environment 2005), and inorganic substances such as mercury, which can bioaccumulate in fish (Feist et al. 2005; Webb et al. 2006). Samples were therefore tested for mercury, PCBs, heptachlor, aldrin, mirex, photomirex, hexachlorocyclohane (α-BHC, β-BHC, γ-BHC), α-chlordane, γ-chlordane, toxaphene, hexachlorobenzene, octachlorostyrene, trans-nonachlor, cis-nonachlor, oxychlordane, *o,p′*-DDT, *p,p′*-DDD, *p,p′*-DDT, and *p,p′*-DDE. Detection limits are summarized in Table 2 (Ministry of the Environment 2005). Hg concentration ([Hg]) and length data were obtained from the Ontario Ministry of Environment for four stable Ontario lake sturgeon populations (Abitibi, Kenogami, Mattagami, and Moose rivers), from the Wisconsin Department of Natural Resources for Wisconsin populations (including Chippewa, Menominee, and Wisconsin rivers; sample size for each Wisconsin waterbody was too small for individual analyses; therefore, data were pooled), and from Quebec's Ministry of Natural Resources for the St. Lawrence River.

Table 2. Levels ($ng \cdot g^{-1}$) in 48 lake sturgeon from the Ottawa River and corresponding detection limits (DL; Ministry of Environment 2005) of selected contaminants.

Compound	Detection limit ($ng \cdot g^{-1}$)	*N*	Average concentration (SD)	Range
Polychlorinated biphenyls (total)	20	36	52.9 (29.7)	20–120
Heptachlor	1			
Aldrin	1			
Mirex	5			
Photomirex	4			
α-BHC	1			
β-BHC	1			
γ-BHC	1			
α-chlordane	2			
γ-chlordane	2			
Toxaphene	50			
Hexachlorobenzene	1			
Octachlorostyrene	1			
trans-Nonachlor	2			
cis-Nonachlor	2			
Oxychlordane	2			
o,p′-DDT	5			
p,p′-DDD	5			
p,p′-DDT	5			
p,p′-DDE	1	35	27.8 (35.4)	2–170
Hg ($\mu g \cdot g^{-1}$)		48	0.29 (0.15)	0.06–0.68

Note: *N*, number of samples > DL; SD, standard deviation.

Statistical analysis

The correlation between relative abundance of lake sturgeon (i.e., CPUE) in each reach as estimated by the two different netting techniques was calculated using Kendall's τ rank correlation. Poisson regression was used to determine if there was an interaction between netting techniques and reach type (commercially harvested or not, impounded or unimpounded); if an interaction existed, then further CPUE analysis using netting technique was conducted separately. Poisson regression was then used to determine if there was a detectable difference in lake sturgeon CPUE between impounded and unimpounded river reaches and reaches with and without a commercial harvest, with netting technique (i.e., FWIN and NSCIN) included as a fixed factor in fitted regression models.

Principal component analysis (PCA) was conducted using $\log_{10}$ total length and $\log_{10}$ age of lake sturgeon from samples. A cumulative distribution graph was constructed from PC1 (an index of size) for impounded and unimpounded river reaches and for commercially harvested and noncommercially harvested reaches; differences in the shape of the curve would identify differences in age–size distribution. von Bertalanffy growth curves were estimated for unimpounded and impounded reaches and reaches with and without a commercial harvest and compared using Kimura's likelihood ratio test (Haddon 2001). Generalized linear models (GLM) was also fitted to $\log_{10}$ total length (dependent) in relation to $\log_{10}$ age and reach type (unimpounded versus impounded, with and without a commercial harvest) as independent factors to assess growth.

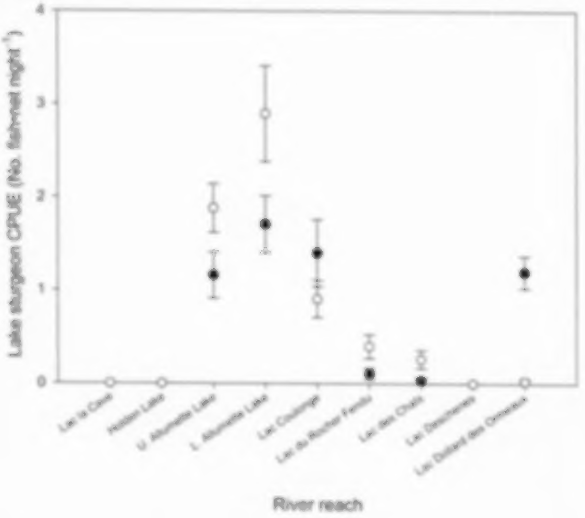
GLMs were fitted to determine if Hg body burden differed between sexes or reach types, using $\log_{10}$[Hg] as the dependent factor and $\log_{10}$ total length and sex or reach type (unimpounded versus impounded, with and without a commercial harvest) as independent factors. To determine if

Table 3. Number, mean total length, and mean weight (standard deviation in parentheses) of lake sturgeon caught by sampling technique in each Ottawa River reach.

River reach	Sampling technique	Year(s)	No. of sturgeon sampled	Mean total length (cm)	Mean weight (g)	No. of nets set
Lac Dollard des Ormeaux	FWIN	2001, 2002	127	76.1 (15.0)	2133 (1591)	106
	NSCIN	2004	1	71.0	1100	40
Lac Deschênes	FWIN	2003	0			24
	NSCIN	2000, 2002	0			80
Lac des Chats	FWIN	2002, 2003	1	73.2	1828	31
	NSCIN	1998	11	109.9 (20.4)	8450 (4773)	42
Lac du Rocher Fendu	FWIN	2002, 2003	3	78.1 (3.1)	2599 (148)	28
	NSCIN	1997, 2000	26	79.8 (16.3)	2655 (1790)	65
Lac Coulonge	FWIN	2002, 2003	42	58.5 (15.3)	1184 (1078)	30
	NSCIN	1998	39	72.8 (18.6)	2079 (1438)	43
Lower Allumette Lake	FWIN	2002, 2003	53	72.9 (13.0)	2007 (1226)	31
	NSCIN	1998	113	83.9 (10.3)	2904 (1258)	39
Upper Allumette Lake	FWIN	1999, 2000	86	81.8 (8.6)	2505 (974)	74
	NSCIN	2001, 2002	256	86.7 (11.2)	3267 (1427)	136
Holden Lake	FWIN	1998	0			36
	NSCIN	2003, 2004	0			48
Lac la Cave	FWIN	1998	0			18
	NSCIN	2004	0			16

Note: FWIN, fall walleye index netting; NSCIN, nearshore community index netting.

Fig. 4. Average (±1 standard error, SE) lake sturgeon (*Acipenser fulvescens*) catch per unit effort (CPUE; number of sturgeon per net night) in different Ottawa River reaches as estimated by fall walleye index netting (FWIN, solid circles) and nearshore community index netting (NSCIN, open circles) from 1998 through 2005.



[Hg] affects lake sturgeon growth. PCA was conducted on $\log_{10}$ total length and $\log_{10}$ weight; GLM was then conducted with PC1 scores as the dependent variable and $\log_{10}$ age and [Hg] as independent factors. GLM was also conducted to determine if there was a relationship between [Hg] and size from different robust lake sturgeon populations (i.e., does Hg accumulate faster in some populations than others?). Total length and [Hg] were $\log_{10}$-transformed.

Statistical analysis was conducted using SYSTAT 11 (SYSTAT Software Inc., Point Richmond, California); Poisson regressions were conducted using S-PLUS 6.2 (Insightful Corporation, Seattle, Washington). Significance was determined at $P = 0.05$.

Results

During the course of the study, we captured 758 lake sturgeon in six of the nine reaches using standardized index netting (Fig. 4): 312 by FWIN and 446 by NSCIN (Table 3), with lake sturgeon CPUE based on FWIN and NSCIN being positively correlated ($r = 0.76$, df = 7, $P = 0.018$) across river reaches (Fig. 4). Lake sturgeon were fully vulnerable to FWIN nets at 80 cm total length (TL); however, FWIN nets were selective for lake sturgeon less than 115 cm TL (Fig. 5). There was also selectivity of the gear due to depth, as significantly smaller lake sturgeon were caught in the deeper depth (5–15 m) strata ($t = 4.07$, df = 125, $P < 0.001$). Lake sturgeon were fully vulnerable to NSCIN nets at 85 cm TL, and NSCIN nets captured larger lake sturgeon than FWIN nets (Fig. 5; i.e., they were not selective to lake sturgeon <115 cm TL). There was an interaction between reach and netting technique (Poisson regression, df = 883, $P <$ 0.001) between impounded and unimpounded reaches; therefore CPUE analysis was conducted separately for each netting technique. Lake sturgeon CPUE was significantly greater in unimpounded reaches than impounded reaches using both FWIN (Poisson regression, df = 376, $P < 0.001$) and NSCIN (Poisson regression, df = 507, $P < 0.001$; Fig. 6). Both size ($\chi^2 = 99.5$, df = 21, $P < 0.001$) and age ($\chi^2 = 65.6$, df = 9, $P < 0.001$) distributions varied between impounded and unimpounded reaches, with smaller, younger fish occurring more frequently in unimpounded reaches (Table 4; Fig. 7*a*). von Bertalanffy growth curves were signifi-

Table 4. von Bertalanffy growth parameters with 95% confidence intervals (CIs) and mean total length (cm) and age (years) with standard deviations (SD) for different reach types.

	River reach			
	Unimpounded	Impounded	Commercially harvested	Unharvested
L_{inf} (95% CI)	113.8 (107.9, 120.0)	147.3 (140.9, 150)	128.9 (121.3, 137.4)	119.1 (101.0, 145.0)
k (95% CI)	0.075 (0.067, 0.085)	0.066 (0.061, 0.073)	0.061 (0.054, 0.069)	0.087 (0.053, 0.131)
t_0 (95% CI)	−2.99 (−2.99, 3.0)	−0.85 (−0.29, −1.36)	−3	−1.54 (0, −3)
Mean total length (SD)	84.1 (16.3)	96.7 (25.4)	87.9 (19.2)	76.1 (16.4)
Mean age (SD)	16.2 (6.3)	17.1 (7.6)	16.9 (6.6)	11.7 (4.5)

Fig. 5. Frequency of different size classes in samples from fall walleye index netting (FWIN, gillnets; solid bars) and nearshore community index netting (NSCIN, trapnets; shaded bars).

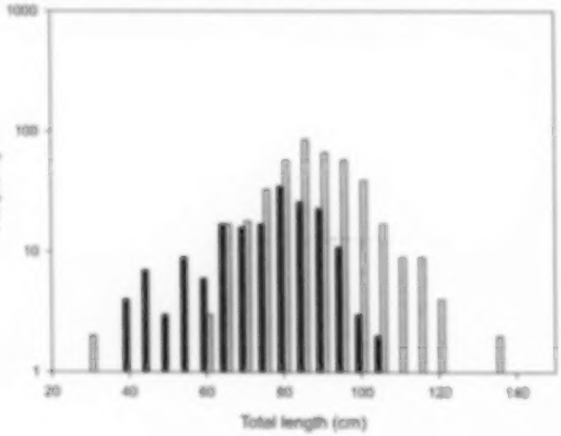
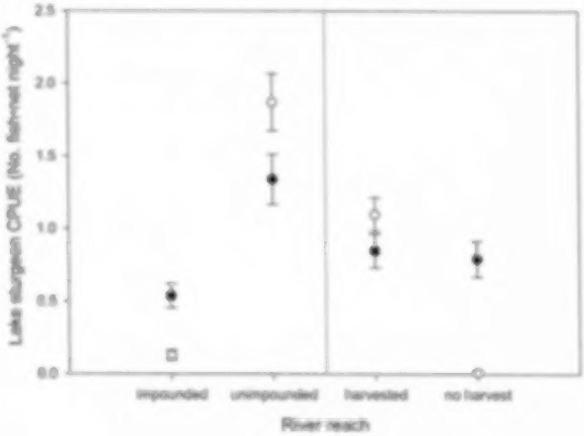


Fig. 6. Average (±1 standard error, SE) lake sturgeon (*Acipenser fulvescens*) catch per unit effort (CPUE; number of sturgeon per net night) as estimated from fall walleye index netting (FWIN; solid circles) and nearshore community index netting (NSCIN; open circles) in impounded and unimpounded reaches and commercially harvested and noncommercially harvested reaches of the Ottawa River.



cantly different between unimpounded and impounded reaches ($F = 55.16$, df = 550, $P < 0.001$; Fig. 8*a*); difference in the curves was influenced primarily by t_0 ($\chi^2 = 9.56$, df = 1, $P = 0.001$). Growth, as estimated by the slope of the regression of $\log_{10}$ length on $\log_{10}$ age, was significantly greater (GLM, $F_{[1,552]} = 33.29$, $P < 0.001$) in impounded than unimpounded reaches.

There was an interaction between reach and netting technique (Poisson regression, df = 883, $P < 0.001$) among reaches with and without a commercial harvest; therefore CPUE analysis was conducted separately for each netting technique. Lake sturgeon CPUE from NSCIN was significantly greater in river reaches with a commercial harvest than without (Poisson regression, df = 507, $P < 0.001$; Fig. 6) but was not significantly different using FWIN (Poisson regression, df = 376, $P = 0.561$). Mean total length of lake sturgeon was significantly greater in river reaches with a commercial harvest than without (t test, $t = 4.088$, df = 745, $P < 0.001$; Table 4). Both size ($\chi^2 = 33.9$, df = 21, $P = 0.037$) and age ($\chi^2 = 28.9$, df = 9, $P = 0.001$) distributions were significantly different between commercially and noncommercially harvested reaches, with populations skewed to larger fish in commercially harvested reaches (Table 4; Fig. 7*b*). von Bertalanffy growth curves were not significantly different between reaches with versus without a commercial harvest ($F = 0.45$, df = 550, $P = 0.72$; Fig. 8*b*). Growth was not significantly different between commercially harvested versus not harvested reaches (GLM, $F_{[1,552]} = 3.66$, $P = 0.056$) nor was the intercept (analysis of covariance, ANCOVA, $F_{[1,553]} = 0.31$, $P = 0.58$). Annual estimated mortality was 18.8% (95% CI, 14.2%, 21.4%) in reaches without a commercial harvest compared with 20.4% (95% CI, 17.0%, 22.1%) for those with a harvest.

Because of the comparatively small number of reaches from which sturgeon were sampled, a factorial analysis of the effect of impounded versus unimpounded, and the presence versus absence of a commercial harvest, is not possible. Growth of lakes sturgeon in noncommercially harvested, impounded reaches was significantly greater than in commercially harvested, impounded reaches (GLM, $F_{[1,113]} = 7.56$, $P = 0.007$). However, the fit of a Poisson model using solely water management reach type (impounded versus unimpounded; deviance residual = 452.5, df = 885), commercial harvest reach type (presence versus absence of a commercial harvest; deviance residual = 67, df = 885) compared with the fit with reach as the sole predictor (deviance residual = 747.5, df = 885), indicates that variation explained by water manage-

Fig. 7. Cumulative distributions of the first principal component (PC1; size) in (*a*) impounded (solid bars, solid line) and unimpounded (shaded bars, dotted line) reaches and (*b*) in reaches with (solid bars, solid line) and without (shaded bars, dotted line) a commercial harvest.

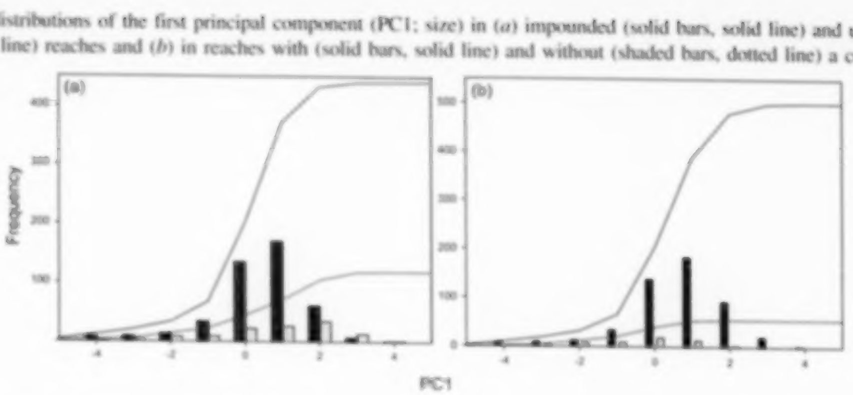


Fig. 8. Fitted von Bertalanffy growth curves for lake sturgeon (*Acipenser fulvescens*) in (*a*) unimpounded reaches (solid circles, solid line) and impounded reaches (open circles, dotted line), and (*b*) commercially harvested (solid circles, solid line) and noncommercially harvested (open circles, dotted line) reaches of the Ottawa River.

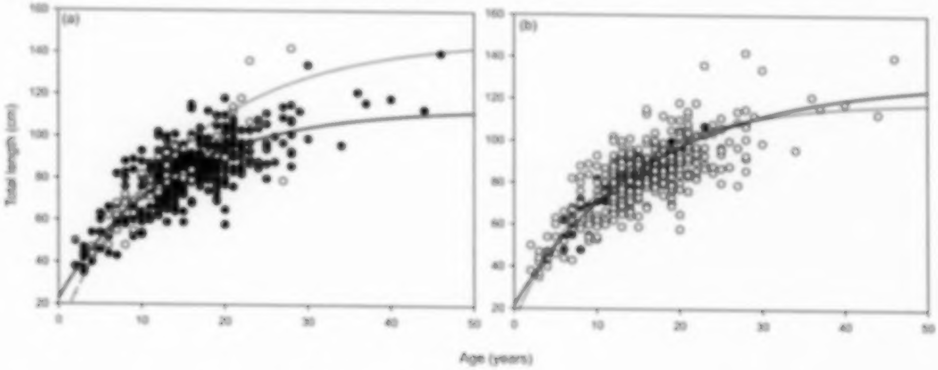
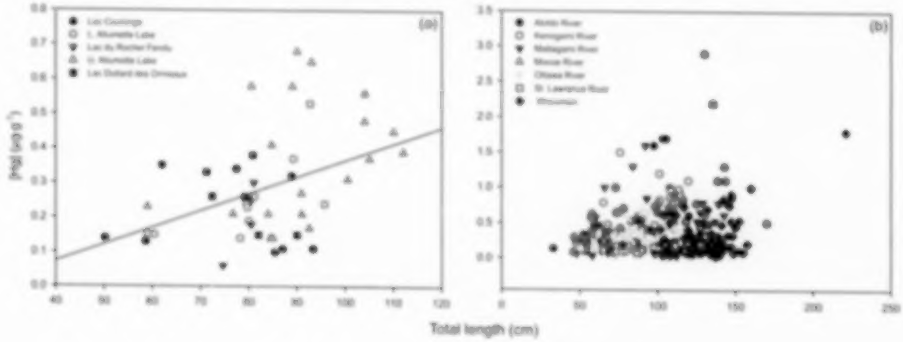


Fig. 9. Mercury concentration ([Hg]) in relationship to total length of lake sturgeon (*Acipenser fulvescens*) from (*a*) various Ottawa River reaches and (*b*) various lake sturgeon populations across North America.



ment regime (60.5%) is a far better predictor of among-reach CPUE than commercial harvest (9.0%).

Of 21 contaminants assayed, only three had at least one sample above detection limit: total PCB ranged from 20 to 120 ng·g^{-1}; DDT (dichloro-diphenyl-trichloroethane) and metabolites ranged from 2 to 170 ng·g^{-1}; and total mercury ranged from 0.06 to 0.68 μg·g^{-1} (Table 2), with mercury being the most commonly detected contaminant. Total mercury concentration increased with total length ($r^2 = 0.17$, df = 47, $P = 0.002$; Fig. 9*a*), with no detectable difference between sexes with respect to either the intercept ($F_{[1,41]} = 0.04$, $P = 0.84$) or the slope ($F_{[1,41]} = 0.04$, $P = 0.84$) of this relationship. There was also no detectable differences between reach type with respect to the intercept ($F_{[1,44]} = 2.68$, $P = 0.109$; $F_{[1,44]} = 0.62$, $P = 0.435$) or slope ($F_{[1,44]} = 2.67$, $P = 0.109$; $F_{[1,44]} = 0.65$, $P = 0.43$) for reaches with or without a commercial harvest and impounded or unimpounded, respectively (Fig. 9*a*). Total length and weight were highly correlated for lake sturgeon sampled for contaminant analysis; PC1 explained 90.9% of the variation. There was no detected relationship between Hg body burden and growth rate (slope ($F_{[14,11]} = 0.71$, $P = 0.71$) or intercept ($F_{[18,1]} = 0.73$, $P = 0.40$)).

Slopes of the relationship between [Hg] and total length among populations across North America were significantly different (GLM, $F_{[6,408]} = 5.043$, $P < 0.001$). However, for a given size, Hg body burden in Ottawa River lake sturgeon was not unusually high against a background of contaminant levels for lake sturgeon in populations (Fig. 9*b*).

Discussion

Despite the reduction in several potential stressors over the past several decades, lake sturgeon in several Ottawa River reaches show little signs of recovery, as evident by low abundance in standard index netting projects and few juveniles within these river reaches. The hypothesis that recovery is being impeded by the already substantially reduced commercial harvest was not supported; reaches still supporting a commercial harvest not only have greater sturgeon CPUE, but also sturgeon in these reaches are, on average, larger than those in reaches without a current harvest, and annual mortality was not significantly greater than in unfished reaches. All reaches at one time supported a commercial harvest, with all fisheries except those in current operation being closed by the early 1990s. Our assumption is that all Ottawa River reaches were depleted to the same level during the uncontrolled harvests of the late 1880s, and there is good evidence that this was a major contributing factor to their historical decline. Unfortunately, accurate, annual harvest levels that would permit us to assess historical biomass (e.g., Secor and Waldman 1999) are not available. Although harvest levels were controlled by quotas after the turn of the century, true, what was though to be "sustainable" (cf. Congdon et al. 1993) quotas were not established until the late 1980s or early 1990s (Brousseau 1987; Fortin et al. 1993). Therefore, although stocks had an opportunity to recover after harvest controls were implemented in the early 1900s, "true" recovery may not have been possible until the early 1990s. Given the age of maturity of lake sturgeon (approximately 25 years for females; Scott and Crossman 1973) and spawning periodicity (4–7 years for females; Roussow 1957; Scott and Crossman 1973; Kempinger 1988), recovery to historical levels, even if all stressors were alleviated, would likely take decades (e.g., >100 years; Secor and Waldman 1999).

Nonetheless, lake sturgeon that were too small for the commercial harvest when it was operational should be currently present in the population and have grown into harvestable size. Yet more than 15 years later, populations in those reaches where commercial operations were eliminated are still dramatically smaller than those in reaches where harvesting currently occurs. Reducing fishing mortality will increase the reproductive potential within the river reach (Boreman 1997); however, increasing survival of adult fish will have limited impact if survival is already relatively high (i.e., >85%; Gross et al. 2002). Thus, although commercial harvesting may well have contributed, perhaps substantially, to historical sturgeon decline, the evidence from this study suggests that the current commercial take is not impeding recovery in the Ottawa River.

Lake sturgeon are susceptible to bioaccumulation of persistent contamination in the environment partially because of their longevity (Feist et al. 2005; Webb et al. 2006). Mercury has been linked to poor reproductive physiology (Feist et al. 2005; Webb et al. 2006) and poor growth and condition (Feist et al. 2005) in lake sturgeon. However, relationships in these studies were weak and very few mature fish were included; the two mature male sturgeon that were included did not display any effects in terms of gonadosomatic index from increased mercury burden (Webb et al. 2006). Although reproductive physiology was not examined during this study, there was no evidence of significant effects of mercury burden on growth or condition, and Hg body burden did not appear to be elevated in impounded versus unimpounded reaches, as was observed in white sturgeon in the Columbia River (Feist et al. 2005). Moreover, contaminant levels in Ottawa River sturgeon are well within the range of concentrations present in considerably more robust sturgeon populations in other North American rivers. As such, there is at present little evidence that sturgeon recovery in the Ottawa River is being impeded by contaminant stress. A similar conclusion was reached for lake sturgeon in the Lower Saskatchewan River (Findlay et al. 1996).

Our results are consistent with the hypothesis that water power management is impeding sturgeon recovery, as has been suggested for white sturgeon (*Acipenser transmontanus*) in the Columbia River (Beamesderfer et al. 1995; Beamesderfer and Farr 1997). Food availability, poor spawning habitat, and changes in flow and temperature were the identified stressors responsible for poor recruitment (Feist et al. 2005). Although relative abundance of lake sturgeon was greater in unimpounded Ottawa River reaches, estimated growth was greater in impounded reaches, suggesting that prey was not limiting for lake sturgeon within these reaches (Parsley et al. 2002). This, combined with the observed reduced abundance, suggests that recruitment during spawning is impaired in impounded reaches.

Lake sturgeon are potamodromous and will migrate long distances, generally for spawning purposes, between foraging, overwintering, and spawning areas (Harkness and Dymond 1961; Rochard et al. 1990; Baker and Borgeson 1999). In the Ottawa River, movement can occur downstream from impounded reaches, but there are no fish ladders to facilitate upstream movement. Movement can occur among the unimpounded reaches as existing rapids are not considered a major barrier, and therefore, there is a concern that the same population was being sampled in different reaches (i.e., pseudoreplication).

Over the course of this study, 794 lake sturgeon were tagged (includes tagging from concurrent work on spawning areas, e.g., Haxton 2006); 628 of these lake sturgeon were tagged in unimpounded reaches. Although recapture rates were low (i.e., <10), all were caught in the same reach in which they were originally sampled (T.J. Haxton, unpublished data). However, lake sturgeon are generally sedentary (Fortin et al. 1993) and are often recaptured in the location in which they were originally tagged (Dumont et al. 1987). Even with the removal of a barrier on a smaller river in Minnesota, lake sturgeon remained within a 32 km section (Borkholder et al. 2002). Lake sturgeon tracked for 2.5 years in the Ottawa River remained within the same section of a reach, despite the potential of extensive movement both upstream and downstream with the absence of barriers (Haxton 2003). These ancillary studies suggest that interreach movement is limited.

Although dams form barriers to migrating species and can limit access to historical spawning areas, sturgeon will spawn at the base of dams (Auer 1996*b*; Cooke and Leach 2004; Duncan et al. 2004). Lake sturgeon are known to spawn at the base of dams in all of the impounded Ottawa River reaches (e.g., Dubreuil and Cuerrier 1950; Haxton 2006). There are several tributaries to the Ottawa River in which lake sturgeon could spawn; however, many of these tributaries are also dammed. Spawning success will depend on flow variability downstream of dams and the presence of suitable spawning habitat (Zakharyan 1971; Auer 1996*b*; Coutant 2004). White sturgeon recruitment, for example, was negatively affected in impounded reaches (Beamesderfer et al. 1995). Mitigation techniques could be employed that could enhance recruitment (LaHaye et al. 1992), e.g., ensuring that adequate flows are provided during spawning through to drift, ensuring that suitable habitat is available immediately downstream or providing passage over dams to historical spawning site (assuming that they have not been altered from impoundment effects).

Unfortunately, factorial analysis could not be conducted because of the lack of nonharvested, unimpounded river reaches in our study. Such reaches may have provided benchmarks for the potential productivity of a river system. There was significant variation in growth and relative abundance among managed reaches with and without a commercial harvest. This would be expected as not all managed reaches are operated under the same water management regime. Lake sturgeon productivity would be expected to vary among peaking, winter reservoir, run-of-the-river, or unimpounded systems. Some water management regimes may not be conducive to recruitment because of the timing of water fluctuation, location of draw from upstream reservoirs (i.e., excessive cooling during spawning affecting survival). Despite the presence of adults in these river reaches (Haxton 2006; T.J. Haxton, unpublished data) and apparently low or zero commercial harvests, recruitment appears limited (based on juveniles sampled in index nets versus unimpounded reaches) and therefore affecting recovery. The greatest potential to enhance lake sturgeon recovery would be to enhance juvenile survival within a reach (Gross et al. 2002). Therefore, although commercial harvest within the river is probably not currently limiting population recovery, its continuance is unlikely going to assist recovery (and may seem counterintuitive), especially in river reaches where natural recruitment appears to already be limited.

The conclusion that sturgeon recovery in the Ottawa River is being impeded primarily by reduced recruitment in impounded reaches should be regarded as tentative. In reaching this conclusion, we have inferred putative causal effects of water power management from variation in indices of sturgeon population condition among different reaches, and clearly, this variation is not solely attributable to the nature of water management in a particular reach. Additional evidence could potentially be provided by similar findings in other riverine sturgeon populations (e.g., sturgeon abundance is reduced in impounded rivers but not unimpounded reaches), but clearly, the lack of similar findings in other systems does not militate against its veracity in the Ottawa River. A much more powerful test of the hypothesis would involve creating additional high quality spawning habitat, ensuring that suitable flows are provided during the spawning period in several impounded and unimpounded reaches; the prediction is then that recruitment relative to levels before habitat creation, recruitment and abundance in the following years, will increase substantially more in impounded than unimpounded reaches. We are currently investigating the possibility of conducting such an experiment on the Ottawa River.

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Rainbow trout (*Oncorhynchus mykiss*) invasion and the spread of hybridization with native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*)

Matthew C. Boyer, Clint C. Muhlfeld, and Fred W. Allendorf

Abstract: We analyzed 13 microsatellite loci to estimate gene flow among westslope cutthroat trout, *Oncorhynchus clarkii lewisi*, populations and determine the invasion pattern of hybrids between native *O. c. lewisi* and introduced rainbow trout, *Oncorhynchus mykiss*, in streams of the upper Flathead River system, Montana (USA) and British Columbia (Canada). Fourteen of 31 sites lacked evidence of *O. mykiss* introgression, and gene flow among these nonhybridized *O. c. lewisi* populations was low, as indicated by significant allele frequency divergence among populations ($\theta_{ST} = 0.076$, $\rho_{ST} = 0.094$, $P < 0.001$). Among hybridized sites, *O. mykiss* admixture declined with upstream distance from a site containing a hybrid swarm with a predominant (92%) *O. mykiss* genetic contribution. The spatial distribution of hybrid genotypes at seven diagnostic microsatellite loci revealed that *O. mykiss* invasion is facilitated by both long distance dispersal from this hybrid swarm and stepping-stone dispersal between hybridized populations. This study provides an example of how increased straying rates in the invasive taxon can contribute to the spread of extinction by hybridization and suggests that eradicating sources of introgression may be a useful conservation strategy for protecting species threatened with genomic extinction.

Résumé : L'analyse de 13 locus microsatellites nous permet d'estimer le flux génique au sein de populations de truites fardées du versant occidental, *Oncorhynchus clarkii lewisi*, et de déterminer les patrons d'invasion des hybrides entre les *O. c. lewisi* indigènes et les truites arc-en-ciel, *Oncorhynchus mykiss*, introduites dans les cours d'eau du bassin supérieur de la Flathead, Montana (É.-U.) et la Colombie Britannique (Canada). Quatorze des 31 sites ne montrent aucun signe d'introgression d'*O. mykiss* et le flux génique entre ces populations non hybrides d'*O. c. lewisi* est faible, tel que l'indique la divergence significative des fréquences d'allèles dans les populations ($\theta_{ST} = 0{,}076$, $\rho_{ST} = 0{,}094$; $P < 0{,}001$). Dans les sites présentant de l'hybridation, l'admixtion d'*O. mykiss* diminue en fonction de la distance vers l'aval à partir d'un site qui contient un rassemblement d'hybrides avec une contribution génétique prédominante (92 %) d'*O. mykiss*. La répartition spatiale des génotypes hybrides à sept locus microsatellites diagnostics indique que l'invasion d'*O. mykiss* est facilitée autant par la dispersion à longue distance depuis le rassemblement d'hybrides que par une dispersion en escalier entre les populations hybrides. Notre étude fournit un exemple qui montre comment les taux accrus d'errance d'un taxon envahissant peuvent contribuer à la diffusion de l'extinction par hybridation et elle laisse croire que l'éradication des sources d'introgression peut être une stratégie utile de conservation pour protéger les espèces menacées d'extinction génomique.

[Traduit par la Rédaction]

Introduction

Hybridization between introduced and native taxa is of increasing conservation and legal concern (Rhymer and Simberloff 1996; Allendorf et al. 2001). The adverse effects of anthropogenic hybridization are sometimes difficult to detect; nevertheless, unique genetic, behavioral, and ecological adaptations in native populations may be lost due to introgression of genes from nonnative taxa (Templeton 1986; Allendorf and Leary 1988; Rhymer and Simberloff 1996). Hybridization may also have indirect consequences for species by affecting their legal conservation status (Allendorf et al. 2004; Haig et al. 2004; Schwartz et al. 2004).

Anthropogenic hybridization is widespread in freshwater fishes, in part due to the long history and pervasiveness of fish translocations and hatchery supplementation in native populations (Leary et al. 1995; Perry et al. 2002). In North America, hybridization with introduced fishes was a significant factor in 38% of fish extinctions (Miller et al. 1989) and is expected to become an even greater threat to biodiversity with increasing rates of species introductions (Fuller et al. 1999). Consequently, conservation of aquatic biodiversity

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will require an understanding of invasion patterns and the mechanisms that promote extinction through hybridization.

Westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) have declined dramatically in distribution primarily because of introgressive hybridization with nonnative rainbow trout, *Oncorhynchus mykiss* (Allendorf and Leary 1988; Liknes and Graham 1988). Matings between *O. c. lewisi* and *O. mykiss* result in the formation of hybrid swarms and the loss of evolved genotypic combinations in *O. c. lewisi* (Allendorf and Leary 1988; Allendorf et al. 2004). Because of the widespread threat of genomic extinction, *O. c. lewisi* have been petitioned for federal listing under the US Endangered Species Act (ESA; US Fish and Wildlife Service (USFWS) 2002) and are recognized as a species of special concern by state and provincial agencies in its native range.

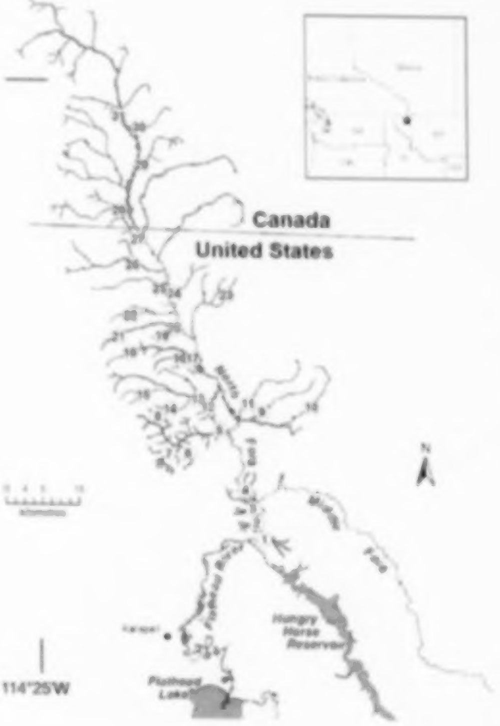
Many invasive taxa possess a relative fitness advantage in novel environments, facilitating population and range expansion (Callaway and Aschehoug 2000). However, when native and invasive taxa hybridize, introgression may spread despite severe fitness penalties in the hybrid progeny (Epifanio and Philipp 2001; Wolf et al. 2001). For example, experimental crosses between *O. mykiss* and *O. c. lewisi* produced hybrids with greatly reduced growth and survival compared with parental types (Allendorf and Leary 1988). Yet, *O. mykiss* introgression has spread rapidly among *O. c. lewisi* populations and does not appear to be effectively constrained by environmental factors (Rubidge et al. 2001; Hitt et al. 2003; Rubidge and Taylor 2005).

The spread of hybridization may also result from increased straying of hybrids. For example, hybridization may prompt invasiveness by disrupting the genetic basis for homing (Bams 1976; Hard and Heard 1999; Ellstrand and Schierenbeck 2000). The rapid spread of hybridization in the Flathead River drainage (Hitt et al. 2003) suggests that hybrids have greater straying rates than native *O. c. lewisi* (Allendorf et al. 2004, 2005), which exhibit strong genetic divergence over small spatial scales (Leary et al. 1988; Taylor et al. 2003). Increased gene flow from hybrids is expected to result in genetic homogenization and a reduction in adaptive divergence among *O. c. lewisi* populations (Lenormand 2002). From a conservation perspective, understanding mechanisms by which the invasive genome spreads among native populations is necessary in order to assess the risk of extinction through hybridization and to inform conservation efforts aimed at identifying and eradicating sources of introgression.

We determined the spatial distribution of hybrid genotypes to test two invasion hypotheses. Under a stepping-stone model of hybrid invasion, introgression spreads via migration between neighboring populations (Kimura and Weiss 1964) and *O. mykiss* admixture declines serially with increasing distance from the source. Alternatively, in a continent–island model, hybrids disperse from a common source to satellite populations. This model predicts no correlation between distance and proportion of admixture or gametic disequilibrium.

The objectives of this study are (*i*) to estimate gene flow among native populations of *O. c. lewisi* in the North Fork Flathead River, Montana, and (*ii*) to test whether the spread of hybridization results from stepping-stone or continent–island patterns of invasion.

Fig. 1. Study area location (star) and sample site identification in Montana (USA) and British Columbia (Canada). See Table 1 for sample site codes.



Materials and methods

Study area

The upper Flathead River drainage originates in southwestern British Columbia and northwestern Montana, encompassing approximately 18 400 km^2. The drainage includes the North Fork, Middle Fork, South Fork, and mainstem Flathead rivers and comprises a major portion of the headwaters of the Columbia River basin. The study area includes tributaries to the North Fork Flathead River, a fifth-order river that flows approximately 160 km south to its confluence with the Middle Fork Flathead River. The North Fork Flathead River drains an area of approximately 4000 km^2 and forms the western boundary of Waterton – Glacier International Peace Park (Fig. 1).

The upper Flathead River drainage is considered a regional stronghold for *O. c. lewisi* (Liknes and Graham 1988), although long-term persistence of this species is uncertain due to widespread hybridization with introduced *O. mykiss* and, to a lesser extent, *Oncorhynchus clarkii bouvieri* (Sage 1993; Hitt et al. 2003). Montana Department of Fish, Wildlife, and Parks (MFWP) stocking records indicate that over 20 million *O. mykiss* individuals were stocked in the lower elevations of the Flathead River drainage (i.e., Flathead Lake and mainstem Flathead River) beginning in the late 1800s and continuing until 1969; however, neither MFWP nor the British Columbia Ministry of Environment

Table 1. Sample site information.

Site code	Site name	Sample size	Latitude	Longitude	Sample year
1	Abbot	34	48.395	–114.041	2004
2	Ivy	20	48.426	–114.068	2004
3	Rabe	30	48.454	–114.081	2004
4	Third	19	48.490	–114.108	2004
5	Langford	30	48.609	–114.196	2004
6	Skookoleel	20	48.557	–114.285	2004
7	Nicola	32	48.556	–114.345	2004
8	Kletomus	32	48.628	–114.383	2004
9	Dutch	32	48.657	–114.070	2004
10	Trout	42	48.669	–113.923	2004
11	Anaconda	31	48.666	–114.113	2004
12	Meadow	25	48.655	–114.235	2004
13	Cyclone	24	48.669	–114.266	2004
14	Deadhorse	22	48.645	–114.348	2004
15	South Fork Coal	26	48.670	–114.431	2004
16	Moran	30	48.747	–114.328	2004
17	Lower Hay	25	48.795	–114.289	2003
18	Upper Hay	24	48.752	–114.476	2003
19	South Fork Red Meadow	26	48.797	–114.376	2004
20	Lower Red Meadow	23	48.808	–114.350	2003
21	Upper Red Meadow	24	48.989	–114.481	2003
22	Moose	30	48.828	–114.483	2004
23	Akokala	32	48.884	–114.199	2004
24	Ford	30	48.878	–114.356	2004
25	Tepee	32	48.887	–114.401	2004
26	Ketchikan	31	48.942	–114.486	2004
27	Colts	25	48.878	–114.356	2003
28	Burnham	25	49.040	–114.536	2003
29	Commerce	25	49.135	–114.477	2003
30	Middlepass	25	49.212	–114.492	2003
31	Parker	20	49.232	–114.556	2003

Note: Sites are coded in approximate order of ascending upstream distance. Latitude and longitude are expressed in decimal degrees.

show record of *O. mykiss* introductions in the North Fork Flathead River. Unintentional introductions of *O. mykiss* likely occurred from Sekokini Springs, a privately owned *O. mykiss* hatchery with a direct outflow to the lower reach of the North Fork Flathead River (near site 1; Fig. 1). Both the MFWP stockings and the unintentional releases were the Arlee strain of *O. mykiss*, which contains a predominant coastal rainbow trout, *Oncorhynchus mykiss irideus*, genetic contribution (R. Leary, University of Montana Conservation Genetics Laboratory, Missoula, MT 59812, unpublished data). Stocking records also indicate the release of *O. c. bouvieri* in a few small headwater lakes in the North Fork drainage, including Red Meadow Lake (near site 21; Fig. 1).

Previous studies (Hitt et al. 2003; Muhlfeld et al. 2003, 2004) have documented a high proportion of *O. mykiss* admixture in Abbot Creek (site 1; Fig. 1) and a decline in *O. mykiss* admixture with increasing upstream distance in the North Fork Flathead River drainage (Hitt et al. 2003). Furthermore, radiotelemetry studies, migrant-trapping data, and redd count surveys have reported high densities of *O. c. lewisi* × *O. mykiss* hybrids in this spawning tributary (Muhlfeld et al. 2003, 2004). These findings prompted MFWP to implement a hybrid removal program in this tributary, beginning in 2002, to reduce sources of hybridization in the upper Flathead River drainage.

Sample collection and DNA analysis

We sampled 31 tributaries to the North Fork Flathead River during late July through early September of 2003 and 2004 (N = 847; Table 1). Fish were captured by electrofishing or angling (sites 10 and 23) in stream reaches ranging from 250 m to 1 km to minimize sampling of related individuals. Total length was recorded and a portion of fin tissue was excised and stored in 95% ethanol. Based on the lengths of the sampled fish and the time of year at which they were collected (i.e., postspawn), all sampled individuals were either resident life history forms or the juvenile progeny of resident or migratory life history forms. Therefore, our samples almost undoubtedly represent individuals produced from natural reproduction in the stream from which they were collected.

DNA was extracted using the Gentra DNA isolation kit (Gentra Systems, Inc., Minneapolis, Minnesota) following the manufacturer's instructions. Thirteen microsatellite loci, seven of which are diagnostic between *O. c. lewisi* and *O. mykiss* (Table 2; Boyer 2006), were amplified following the condi-

Table 2. Distribution of genetic diversity in *Oncorhynchus clarkii lewisi* populations.

Locus	H_S	θ_{IS}	θ_{ST}	ρ_{ST}	No. of alleles
OMM1019	0.497	–0.070 (0.035)	0.072** (0.021)	0.053**	4
OMM1050	0.090	–0.040 (0.078)	0.040** (0.019)	0.038**	2
OMM1060	0.061	–0.078 (0.015)	0.038** (0.014)	0.040**	2
OMY0004	0	—	—	—	1
SFO8	0.361	0.010 (0.077)	0.088** (0.029)	0.091**	4
SSA456	0	—	—	—	1
OGO8	0.033	–0.037 (0.015)	0.021** (0.012)	0.010**	2
OMM1037-1	0.413	–0.076 (0.043)	0.131** (0.056)	0.137**	6
OMM1037-2	0	—	—	—	1
SSA311	0.143	–0.070 (0.037)	0.076** (0.044)	0.105**	4
OGO5	0	—	—	—	1
OCL2	0.581	0.002 (0.050)	0.047** (0.017)	0.062**	5
ONEµ14	0.582	0.020 (0.052)	0.072** (0.023)	0.092**	15
Overall	0.212	–0.024 (0.019)	0.076** (0.012)	0.094**	

Note: Loci above the broken line are diagnostic between *O. c. lewisi* and *O. mykiss*. Values for θ_{IS} and θ_{ST} are jackknifed mean and standard error (in parentheses). Significance assessed after sequential Bonferroni corrections; **, $P < 0.01$.

tions described by the original authors (*SFO8*, Angers et al. 1995; *SSA311*, *SSA456*, Slettan et al. 1995; *ONEµ14*, Scribner et al. 1996; *OCL2*, Condrey and Bentzen 1998; *OGO5*, *OGO8*, Olsen et al. 1998; *OMY0004*, Holm and Brusgaard 1998; *OMM1019*, *OMM1037-1*, *OMM1037-2*, *OMM1050*, *OMM1060*, Rexroad et al. 2002). Polymerase chain reaction (PCR) was conducted in a PTC-100 thermocycler (MJ Research Inc., Waltham, Mass.) using fluorescently labeled primers, and amplification products were electrophoresed through 7% polyacrylamide gels and visualized using a Hitachi FMBIO-II fluorescent imager (MiraiBio, Inc., Alameda, California). Allele sizes were determined using MapMarkerLOW size standards (BioVentures, Inc., Murfreesboro, Tennessee) and Hitachi FMBIO-II software (MiraiBio, Inc. 1999). Previously scored individuals were included on each gel as controls to ensure consistent allele scoring across populations.

Genetic variation within and among populations

Deviations from Hardy–Weinberg proportions were examined using exact tests in which *P* values were estimated using the Markov Chain algorithm of Guo and Thompson (1992). Genotypic differentiation at each locus and between all pairwise *O. c. lewisi* population comparisons was assessed with log-likelihood (*G*) based exact tests (Goudet et al. 1996) using the default parameters for Markov chain tests in program GENEPOP. Sequential Bonferroni adjustments (Rice 1989) were used to assess statistical significance for simultaneous tests with an initial α level of 0.05.

Unbiased estimates of Wright's (1951) *F* statistics (θ_{IS}, θ_{ST}; Weir and Cockerham 1984) were assessed using programs GENEPOP (version 3.1; Raymond and Rousset 1995) and FSTAT (version 2.9.3; Goudet 1995). Additionally, ρ_{ST} (Rousset 1996), a weighted analogue of R_{ST} (Slatkin 1995), was calculated to account for differences in allele size under a stepwise mutation model. We used the allele size permutation procedure in program SPAGeDi (Hardy and Vekemans 2002; Hardy et al. 2003) to test whether mutations contributed significantly to population divergence. This test randomly permutes allele sizes observed at a given locus among allelic states to obtain a distribution of ρ_{ST} values. Under the null hypothesis (i.e., $\theta_{ST} = \rho_{ST}$), the ρ_{ST} values computed after allele size permutation are equal to the observed ρ_{ST} value from the actual data set. Alternatively, if stepwise mutations contribute to population divergence, the observed ρ_{ST} value will be significantly larger than the mean of the permuted ρ_{ST} values (one-tailed test).

Mantel tests in FSTAT were used to test for isolation by distance (Wright 1943) among *O. c. lewisi* populations using $\theta_{ST}/(1 - \theta_{ST})$ as an unbiased measure of genetic differentiation and fluvial distance (km) as a measure of geographic distance. Following a significant Mantel test result, a second Mantel test was performed on the residuals from the fitted regression line against fluvial distance. At migration–drift equilibrium, residuals are expected to increase with distance, as drift, rather than gene flow, becomes the dominant force at greater distances.

Individual and population admixture

Genetic data should be examined at both the individual and population levels to accurately describe the history of hybridization in populations and determine whether a site contains a hybrid swarm or mixed population of parental types and their hybrids. Using diagnostic codominant markers, such as microsatellites, population admixture is calculated as the proportion of diagnostic *O. mykiss* alleles found among individuals within a population. To estimate individual admixture, we calculated a hybrid index based on genotypes at the seven diagnostic loci. This index ranges from 0 (no *O. mykiss* alleles) to 1 and is calculated by dividing the total number of diagnostic *O. mykiss* alleles in an individual by $2X$ (where X equals the number of diagnostic loci). First-generation hybrids between *O. mykiss* and *O. c. lewisi* have a hybrid index of 0.5 and are heterozygous for alleles from the parental taxa at all loci. Statistical power to differentiate between parental types and early generation hybrids is high with seven diagnostic codominant markers. For example, the probability that a first-generation backcross would be misclassified as an F_1 hybrid is less than 0.01 (Boecklen and Howard 1997). However, reliable discernment between parental types and later generation backcrosses requires many diagnostic loci (Floate et al. 1994); consequently, our hybrid index likely overestimates parental types and underestimates the number of individuals of hybrid ancestry.

We used the Bayesian model in program STRUCTURE (Pritchard et al. 2000; Falush et al. 2003) to estimate population admixture based on genotypes at all 13 microsatellite loci. We defined the number of parental populations (K) to be 2 (i.e., *O. mykiss* and *O. c. lewisi*) and 22 individuals with a hybrid index of 1 were designated as priors in the model and assigned the highest admixture value of $q = 1$ (i.e., we forced the model to consider these individuals as *O. mykiss*). To test the validity of using these individuals as priors, we ran the model without priors and obtained nearly identical results ($r^2 > 0.99$). We concluded that these individuals are accurate representations of *O. mykiss* and present results from the model using priors. Population admixture is calculated as the arithmetic mean of q values for individuals in a population. Population admixture proportions obtained from program STRUCTURE (q) were highly correlated ($r^2 > 0.99$) with admixture estimates from the seven diagnostic loci (Boyer 2006); however, estimates of q account for allele frequency differences between taxa at an additional six nondiagnostic loci.

High mutation rates in microsatellites and the high degree of intraspecific genetic variation among *O. c. lewisi* populations increases the likelihood that some populations may have rare alleles typically characteristic of *O. mykiss* (i.e., homoplasy). We differentiated between homoplasy in *O. c. lewisi* populations and low proportions of admixture by examining the number and distribution of diagnostic *O. mykiss* alleles across loci. Hybridization is expected to result in approximately equal rates of introgression throughout the genome at selectively neutral loci. Consequently, a relatively high frequency of an allele diagnostic for *O. mykiss* at a single locus is likely evidence of homoplasy and not hybridization (Forbes and Allendorf 1991). Alternatively, the presence of more than one diagnostic *O. mykiss* allele among individuals at a sample site was assumed to indicate hybridization.

Nonrandom mating and gametic disequilibrium

From a conservation perspective, it is important to discern between panmictic hybrid swarms and recently hybridized populations. In the latter case, individuals from the native parental taxon still exist and removal of hybrids may be a feasible strategy to reduce further introgression (Allendorf et al. 2001). Tests for gametic disequilibria (i.e., nonrandom association of genotypes between loci) in hybridized sites were used to discern between hybrid swarms and recently introgressed populations (Forbes and Allendorf 1991). When genetically divergent taxa interbreed, gametic disequilibrium will initially be high. For unlinked loci, disequilibrium will decay by one-half each generation under Hardy–Weinberg conditions. The presence of gametic disequilibrium in hybridized populations may indicate one or more of the following: (*i*) the hybridization event is relatively recent and the site contains a mixed population of parental types and their hybrids, (*ii*) the loci are linked, and (or) (*iii*) selection is acting on certain genotypes. Alternatively, the absence of statistically significant gametic disequilibrium indicates either recent introgression by post-F_2 individuals (i.e., low power of detection) or that mating among hybrids has occurred for many generations. We evaluated gametic disequilibria for all pairwise diagnostic locus comparisons within populations using the Markov Chain method implemented in GENEPOP and assessed significance using sequential Bonferroni-adjusted error rates ($\alpha = 0.05$/number of pairwise comparisons within a sample; Rice 1989).

We employed an additional method to describe the distribution of hybrid genotypes within a population. We tested whether *O. mykiss* alleles were randomly distributed among individuals (i.e., hybrid swarm) by comparing the observed frequency of hybrid indices in a population with a binomial probability distribution based on the proportion of admixture estimated from allele frequencies at the diagnostic loci. Significant departures from expected values were assessed with a χ^2 test ($\alpha = 0.05$). It is important to note that power to detect significant departures from binomial genotypic expectations is low in populations with small amounts of *O. mykiss* admixture. In these situations, failure to reject the null hypothesis of random distribution of *O. mykiss* alleles among individuals does not necessarily indicate that the population is a hybrid swarm. Rather, the sample may comprise a mixed population of nonhybridized *O. c. lewisi* and one or two hybrids that are later-generation backcrosses to *O. c. lewisi*.

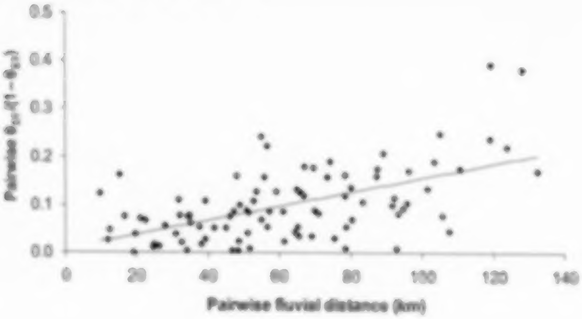
Spatial pattern of hybrid invasion

We tested between two a priori migration models to determine the pattern of hybrid invasion within the drainage. The spatial pattern of introgression is determined by the pattern of migration and the proportion of *O. mykiss* admixture in the migrants. Under a stepping-stone model of genetic invasion (Kimura and Weiss 1964), migration occurs between adjacent populations. This model predicts a negative correlation between distance from a source population and proportion of *O. mykiss* admixture, a serial dilution of diagnostic *O. mykiss* alleles from low elevation to higher elevation hybridized sites, and the presence of F_1 hybrids (i.e., gametic disequilibria) in lower elevation sites. Furthermore, introgression is expected to spread at a slower rate as individual migration distance is shorter and neighboring populations have similar admixture proportions.

Alternatively, a continent–island model predicts an equal probability of migration among sites, independent of distance from the source population. In this model, we expect no spatial autocorrelation for *O. mykiss* admixture, diagnostic *O. mykiss* alleles, or the presence of F_1 hybrids. Additionally, the incidence and proportion of *O. mykiss* admixture among populations are expected to increase at a faster rate than they would by stepping-stone migration because migrants disperse from a common source with a high proportion of admixture.

Straight-line distances may inaccurately characterize spatial processes in riverine environments. Therefore, fluvial measurements were used to calculate distance between all sample sites using ArcView® Spatial Analyst (ESRI, Redlands, California). Correlations between fluvial distance and

Fig. 2. Isolation by distance analyses for *Oncorhynchus clarkii lewisi* populations in the North Fork Flathead River drainage (Mantel, $r = 0.32$, $P < 0.001$).



proportion of *O. mykiss* introgression were assessed using Pearson's correlation coefficient.

Results

O. c. lewisi population genetic structure

Fourteen of 31 sites showed no evidence of *O. mykiss* introgression, and power to detect as little as 1% *O. mykiss* genetic contribution in a hybrid swarm was at least 0.94 and generally exceeded 0.97 (Boecklen and Howard 1997). Of the 14 nonhybridized populations, none showed evidence of homoplasy, thereby increasing our confidence in classifying these individuals as nonhybridized *O. c. lewisi*.

Genetic variation within *O. c. lewisi* populations was relatively low. Four of 13 loci analyzed were monomorphic in *O. c. lewisi* populations (Table 2), and heterozygosities within populations ranged from 0.188 (site 6) to 0.234 (site 29). Genotypic frequencies generally conformed to expected Hardy–Weinberg proportions. Skookoleel Creek (site 6) was the only site that showed a significant overall departure from expected Hardy–Weinberg genotypic proportions ($\alpha = 0.05$). After correcting for multiple tests (Rice 1989), only Burnham Creek (site 28) showed a significant departure from expected Hardy–Weinberg proportions with an excess of heterozygotes at *SFO8*.

Log-likelihood (G) based exact tests for *O. c. lewisi* population differentiation indicated significant differences in genotypic frequencies at each of the nine polymorphic loci ($P < 0.01$) and over all loci combined ($\theta_{ST} = 0.076$, $\rho_{ST} = 0.094$, $\alpha' = 0.05/9 = 0.0056$; Table 2). All pairwise tests for population differentiation (θ_{ST} and ρ_{ST}) were significant at the $\alpha = 0.05$ level, and 81 of 91 pairwise comparisons were significant after correcting for multiple comparisons ($\alpha' = 0.05/9 = 0.0056$). Values of θ_{ST} and ρ_{ST} were similar at all nine polymorphic loci (Table 2), and allele size permutation tests revealed no significant contribution of stepwise mutations to *O. c. lewisi* population divergence ($P > 0.1$). Mantel tests showed evidence for isolation by distance (i.e., stepping-stone migration) among *O. c. lewisi* populations (Mantel, $r = 0.32$, $P < 0.001$; Fig. 2), and residuals from the fitted regression line were not correlated with distance (Mantel, $r < 0.001$, $P > 0.1$).

Table 3. Mean percentage admixture from *Oncorhynchus mykiss* (q) at sample sites.

Code	Site	N	q (SD)	D
1	Abbot	35	91.6 (0.01)	0
2	Ivy	20	49.3 (0.32)	3 ***
3	Rabe	30	49.1 (0.17)	6 ***
4	Third	19	65.8 (0.33)	0 ***
5	Langford	30	33.1 (0.27)	6 ***
7	Nicola	32	1.8 (0.04)	0 *
9	Dutch	32	13.0 (0.13)	0
10	Trout	42	1.0 (0.02)	0
11	Anaconda	31	20.6 (0.22)	21 ***
12	Meadow	25	3.5 (0.06)	0 ***
13	Cyclone	24	11.6 (0.15)	2 ***
15	South Fork Coal	26	0.6 (0.02)	0
17	Lower Hay	25	1.4 (0.05)	0
19	South Fork Red Meadow	26	0.3 (0.01)	0
20	Lower Red Meadow	23	2.2 (0.07)	0
21	Upper Red Meadow	24	12.2 (0.20)[a]	0 ***
25	Tepee	32	1.3 (0.03)	0

Note: SD, standard deviation; D, the number of pairwise diagnostic locus comparisons in significant gametic disequilibria ($\alpha' = 0.05/21 = 0.0024$). Hybridized populations with significant nonrandom association of *O. mykiss* alleles among individuals are indicated by asterisks: *, $P < 0.05$; ***, $P < 0.001$.

[a] Denotes probable genetic contribution from Yellowstone cutthroat trout (*O. c. bouvieri*).

Hybrid populations

Hybridization was detected in 17 of 31 sample sites, and the proportion of *O. mykiss* admixture ranged from 0.3% to 91.6% (Table 3). In addition to *O. mykiss* introgression, we detected alleles that likely indicate *O. c. bouvieri* introgression at the Upper Red Meadow site. Three alleles at *OMYOO04* were not found at any other site in the study area and are 26 base pairs longer than the next shortest allele length, suggesting they are not *O. c. lewisi* or *O. mykiss* polymorphisms. Furthermore, paired interspersed nuclear element (PINE) genetic analysis (Spruell et al. 2001; Kanda et al. 2002) confirmed *O. c. bouvieri* introgression in previous samples collected near this site (Muhlfeld et al. 2003). PINE analysis examines six diagnostic nuclear DNA fragments for *O. c. lewisi*, seven for *O. mykiss*, and nine for *O. c. bouvieri*.

All 13 loci were polymorphic in the hybridized populations, and heterozygosities within populations ranged from 0.101 (site 10) to 0.648 (site 3). Exact tests for conformity to Hardy–Weinberg proportions revealed a significant deficit of heterozygotes in nine of 17 (53%) sample sites when analyzing across loci within populations (Table 4). Within loci, 28 of 32 (88%) significant departures from Hardy–Weinberg proportions resulted from a deficit of heterozygotes (Table 4).

Pairwise tests for gametic disequilibrium at the seven diagnostic loci within hybridized sites rejected the null hypothesis of independence in 38 of 357 comparisons ($\alpha' = 0.05/21$ pairwise comparisons within a site $= 0.0024$). Five of 17 hybridized sites displayed significant gametic disequilibria at two or more diagnostic loci (Table 3).

Chi-square tests revealed a nonrandom distribution of *O. mykiss* alleles among individuals in nine of 17 hybridized

Table 4. θ_{IS} values and deviations from Hardy–Weinberg proportions in hybridized populations.

			θ_{IS}					
Code	Site	*N*	*OMM1019*	*OMM1050*	*OMM1060*	*OMY0004*	*SFO8*	*OMM1037-1*
1	Abbot	34	0.053	0.022	0.017	0.031*	–0.024	–0.032
2	Ivy	20	0.194***	0.329***	–0.043	–0.140	0.174*	0.064*
3	Rabe	30	–0.012	–0.027	0.092	–0.094	–0.021*	–0.075
4	Third	19	0.132	0.097	0.236	0.157*	0.207**	0.088
5	Langford	30	0.000	0.060	0.082	0.172	0.057	–0.067
7	Nicola	32	–0.169	—	0.076	—	—	–0.084
9	Dutch	32	0.028	0.129	–0.192	–0.139	–0.022	0.003
10	Trout	42	—	—	—	—	–0.006	—
11	Anaconda	31	–0.048	–0.020	0.085	0.092	–0.071	–0.036
12	Meadow	25	0.160	–0.120	–0.029	–0.011	–0.091	–0.158
13	Cyclone	24	–0.245	–0.040	–0.192	–0.066	–0.025	0.107
15	South Fork Coal	26	0.025	–0.064	–0.047	—	—	0.096
17	Lower Hay	25	0.096	—	–0.029	—	0.145	–0.062
19	South Fork Red Meadow	26	–0.028	–0.020	–0.042	—	–0.084	0.194
20	Lower Red Meadow	23	0.155	–0.031	–0.086	—	0.197	–0.341
21	Upper Red Meadow	24	0.057	–0.011	0.292	0.229	0.188*	–0.025
25	Tepee	32	–0.045	—	—	—	0.068	–0.123

Note: Significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

sites (Table 3). This test confirmed the results of the gametic disequilibrium test and identified nonrandom mating in four additional populations. We expect this test to be more sensitive to detecting nonrandom mating than the pairwise locus test for gametic disequilibria because it considers the distribution of *O. mykiss* alleles at all seven diagnostic loci simultaneously.

The distribution of hybrid indices is useful for determining whether a site contains a hybrid swarm or mixed population of hybrids and *O. c. lewisi*. In Abbot Creek, all fish possessed hybrid indices ranging from 0.8 to 1, and the distribution of *O. mykiss* alleles among individuals conformed to the expected random binomial distribution (χ^2_{12} = 15.09, P = 0.24; Table 3). This sample, therefore, appears to have come from a hybrid swarm with a predominant (92%) *O. mykiss* genetic contribution. Three other sites contained individuals with hybrid indices of 0.8 or greater (Third Creek, N = 10; Ivy Creek, N = 7; Rabe Creek, N = 1); however, the nonrandom distribution of *O. mykiss* alleles among individuals from these samples ($P < 0.001$; Table 3) indicates that these sites either have recently been hybridized or contain two or more populations with different admixture proportions.

Spatial pattern of hybrid invasion

Among hybridized sites, *O. mykiss* admixture was greatest in Abbot Creek (q = 91.6%; Table 3). Furthermore, only nine of 58 (15.5%) diagnostic *O. mykiss* alleles found among hybridized populations were not detected in the Abbot Creek sample. These nine *O. mykiss* alleles were present in hybridized populations within 65 fluvial km from this site and generally occurred at low frequencies. In only one instance did an *O. mykiss* allele not sampled in Abbot Creek occur at another site at a frequency greater than 0.1 (*OMM1050**328 in Third Creek; frequency = 0.18).

The significant negative correlation between the proportion of *O. mykiss* admixture and fluvial distance from Abbot Creek (r^2 = 0.88, $P < 0.001$; Fig. 3) is consistent with a stepping-stone pattern of hybrid invasion. Furthermore, sites with low proportions of admixture were located furthest from Abbot Creek and contained individuals with genotypes characteristic of later-generation backcrosses to *O. c. lewisi*.

We also found evidence that hybridization is spreading via long-distance migration of individuals with a high proportion of admixture. Five individuals in Anaconda Creek and two individuals in Cyclone Creek possessed genotypes characteristic of first-generation matings (i.e., F_1 hybrids) between *O. c. lewisi* and individuals with a hybrid index of 0.8 or greater (Fig. 4). The distribution of hybrid indices among individuals at these two sites indicated they were not hybrid swarms (Table 3) and none of the F_1 hybrids possessed *O. c. lewisi* alleles not detected within the population in which they were collected. One of the F_1 hybrids sampled in Anaconda Creek possessed a diagnostic *O. mykiss* allele not found in Abbot Creek (*OMY0004**158). Third Creek was the only other population in which we detected this allele (frequency = 0.079).

Discussion

Anthropogenic hybridization is one of the most underestimated threats to aquatic biodiversity because of the difficulty in detecting introgression and the complexity of measuring fitness effects of outbreeding depression (Rhymer and Simberloff 1996; Allendorf et al. 2001; Epifanio and Philipp 2001). Indeed, the ecological and evolutionary consequences of anthropogenic hybridization are just beginning to be understood (Olden et al. 2004). Here, we provide evidence supporting the hypothesis that anthropogenic hybridization can disrupt homing behavior and increase the rate at which biodiversity is lost through homogenization of divergent gene pools in the native taxon.

Our results indicate that *O. mykiss* introgression in the North Fork Flathead River drainage is spreading via long-

OMM1037-2	*SSA456*	*OGO8*	*OGO5*	*SSA311*	*OCL2*	*ONEµ14*	All
—	0.294	0.135	—	–0.018**	–0.059	0.576***	0.074***
0.321	0.281	0.287**	–0.027	0.133**	0.231	0.227	0.164***
0.740***	0.131	–0.032	–0.018	–0.041	0.078*	0.131*	0.050***
0.297	–0.053	0.452*	—	0.412**	0.564***	0.271*	0.240***
0.114	–0.139	0.068	—	0.105	0.135	0.428***	0.092*
—	—	–0.033	—	–0.038	–0.146	0.095	–0.043
–0.088	0.441	–0.054	—	0.119	0.370***	0.028	0.064*
–0.025	—	–0.006	—	—	–0.060*	–0.026	–0.038
0.437	–0.111	0.286	—	0.129	0.451***	0.184	0.116***
—	–0.021	–0.045	—	–0.091	0.170	–0.150	–0.031
0.418	–0.179	–0.100	—	0.189	0.007	0.145	0.009
—	—	1*	—	0.048	0.530*	0.263**	0.208**
—	—	–0.011	—	—	–0.253	–0.016	–0.040
—	—	—	—	—	–0.171	–0.078	–0.061
—	—	—	—	0.148	–0.244*	0.050	–0.037
0.284	0.130	0.367**	—	0.209	0.395***	0.063	0.173***
—	—	–0.051	—	–0.038	0.186*	0.229*	0.063

Fig. 3. Decrease in population *Oncorhynchus mykiss* admixture (q) with increasing distance from Abbot Creek. Quadratic regression line was fit using the least squares method ($r^2 = 0.88$, $P < 0.001$).

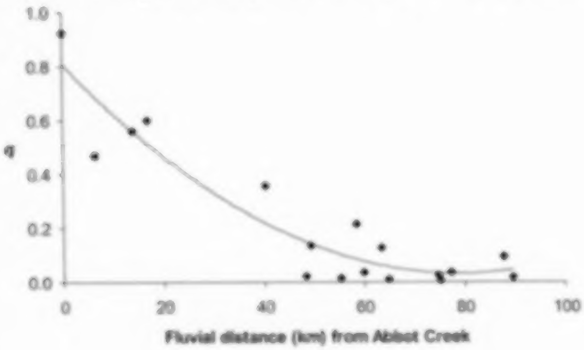
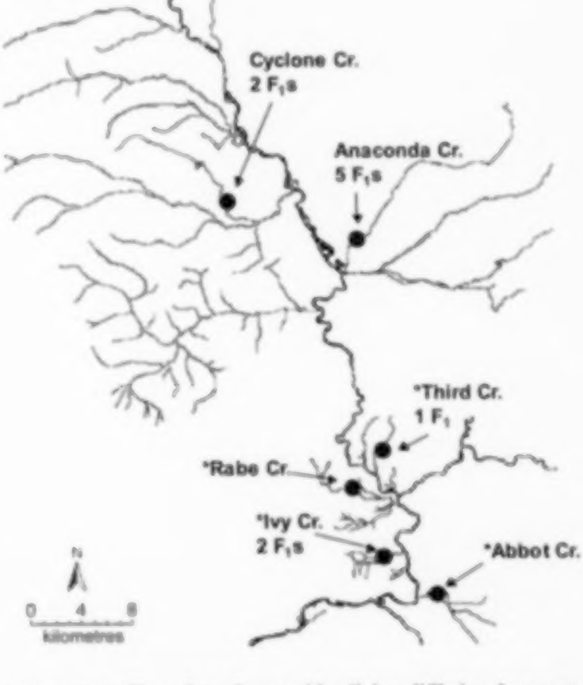


Fig. 4. Distribution of F_1 hybrids in the study area. Sites containing individuals with a hybrid index of 0.8 or greater are marked with an asterisk (*).



distance dispersal from a downstream source and stepping-stone dispersal between hybrid populations. Although we did not directly test for the effect of varying proportions of admixture on straying rates, the spatial distribution of hybrid genotypes strongly suggests that the observed dispersal from the hybrid swarm in Abbot Creek is much greater than estimated rates of gene flow among *O. c. lewisi* populations in the study area. This behavioral difference in homing ability between hybrids and *O. c. lewisi* has been reported in other studies in the Flathead and Kootenai drainages (Rubidge et al. 2001; Hitt et al. 2003) and is likely an important mechanism promoting the spread of *O. mykiss* introgression.

Our θ_{ST} and ρ_{ST} analyses revealed significant genotypic divergence among *O. c. lewisi* populations and contribute insight into the factors responsible for population subdivision. Mutational processes at microsatellite loci tend to follow a stepwise mutation model in which populations with alleles differing by a few repeat units will have experienced more recent gene flow than those with alleles differing by many repeat units (Slatkin 1995). ρ_{ST} uses information on the length of alleles at microsatellite loci and generally provides less biased estimates of genetic divergence at loci with high heterozygosity. In contrast, traditional F statistics (i.e., θ_{ST})

do not consider allelic identity and may underestimate divergence when using highly polymorphic loci such as microsatellites (Hedrick 1999). Permutation tests revealed no significant difference between estimates of θ_{ST} and ρ_{ST} in our microsatellite data set. This result suggests that, at the geographic scale of this study, genetic divergence between populations is caused mainly by drift and that migration rates are larger than mutation rates at the examined loci.

Mantel tests supported a stepping-stone model of dispersal among *O. c. lewisi* populations; however, the lack of increase in residuals with distance suggests that populations in the North Fork Flathead drainage are not at migration–drift equilibrium. This result may be due to recent colonization of streams following the retreat of glaciation or caused by complex migration patterns that do not follow a simple stepping-stone or continent–island model (Taylor et al. 2003).

Indirect measures of migration from *F* statistics are based on a number of simplifying assumptions, some or all of which may be unrealistic in natural populations (Whitlock and McCauley 1999). Nevertheless, these estimates provide insight into the amount of migration among populations and are commonly used for conservation purposes (Mills and Allendorf 1996). Under the assumptions of a continent–island model, the amount of genotypic divergence observed among *O. c. lewisi* populations in the North Fork Flathead drainage (θ_{ST} = 0.076) is equivalent to approximately three migrants per generation (Wright 1931). However, the assumption of no spatial structure to migration may not be valid in our study area because of evidence of isolation by distance (i.e., stepping-stone migration) among *O. c. lewisi* populations. Gene flow between adjacent populations is less effective at reducing genetic divergence as migrants are genetically more similar to each other. Consequently, three migrants per generation may be a conservative estimate of straying rates for *O. c. lewisi* in this drainage.

Our data indicate that Abbot Creek is a significant source of introgression in the upper Flathead River system. This site contains the greatest proportion of admixture and the majority (85%) of *O. mykiss* alleles in the study area were detected in the Abbot Creek sample, suggesting that *O. mykiss* initially colonized this site prior to upstream expansion. Furthermore, the lack of significant gametic disequilibrium indicates that this hybrid swarm has existed for several generations.

In contrast to other drainages in which widespread stocking of *O. mykiss* has resulted in multiple sources of introgression, *O. mykiss* introductions in the upper Flathead River drainage have occurred almost exclusively in the mainstem Flathead River and Flathead Lake. As a result, the observed spatial distribution of introgression in our study area is ultimately attributable to upstream invasion of *O. mykiss*. Although *O. mykiss* alleles were present in over half of our sites, individuals with genotypes characteristic of parental *O. mykiss* were detected at only three sites, suggesting that introgression is readily spreading despite low numbers of parental *O. mykiss* in the system.

Our data suggest that both stepping-stone and continent–island patterns of invasion facilitate the spread of *O. mykiss* introgression in the system. The serial decline in *O. mykiss* admixture with upstream distance from Abbot Creek is consistent with a stepping-stone model of hybrid invasion. However, we also found F_1 hybrids in sites where no parental *O. mykiss* or highly admixed hybrids were detected, suggesting long-distance dispersal from sites with a high proportion of *O. mykiss* admixture. Although we can not rule out the possibility that interbreeding between local populations of *O. mykiss* and *O. c. lewisi* produced the F_1 hybrids found in Cyclone and Anaconda creeks, we consider this scenario highly unlikely, as previous genetic surveys (Hitt et al. 2003; Muhlfeld et al. 2003) also failed to detect parental *O. mykiss* or highly admixed hybrids at these sites. The most probable explanation for the presence of F_1 hybrids at these sites is recent straying and gene flow from the hybrid swarm in Abbot Creek.

The significant deficit of heterozygotes and gametic disequilibrium in hybridized sites most likely indicate either recent hybridization, positive assortative mating between hybrids and *O. c. lewisi*, or possibly selection against hybrids. Allendorf and Leary (1988) reported reduced survival and growth of F_1 hybrids between *O. c. lewisi* and *O. mykiss* in a hatchery environment, suggesting outbreeding depression in hybrids. However, even with severe fitness penalties against hybrid progeny, hybrid swarms may still result because of the unidirectional nature of hybridization (i.e., progeny of hybrids are hybrids; Epifanio and Philipp 2001). In our study area, continued invasion from hybrids and weak spatial and temporal segregation in spawning indicates that sites presently containing mixed populations of hybrids and *O. c. lewisi* will inevitably become hybrid swarms and sites containing nonhybridized *O. c. lewisi* are at high risk of invasion and subsequent introgression.

The spread of introgression among *O. c. lewisi* populations is of conservation concern for several reasons. Increased gene flow from hybrids is expected to homogenize genetic variability among *O. c. lewisi* populations. The geographic range of *O. c. lewisi* is the largest of all cutthroat trout subspecies and many populations contain rare alleles that likely confer local adaptations necessary for long-term persistence (Allendorf and Leary 1988). Continued introgression between introduced and native trout taxa leads to the homogenization of genetic variation and a reduction in both biodiversity and adaptive genetic divergence (Lenormand 2002; Olden et al. 2004).

MFWP's management plan for restoring native *O. c. lewisi* includes eradication of nonnative salmonid populations to reduce the spread of hybridization. The pattern of introgression in the North Fork Flathead River drainage indicates that the spread of hybridization is facilitated by migration of individuals with a high proportion of *O. mykiss* admixture from one or more source populations. Consequently, removal of hybrid source populations has the potential to be an effective management strategy for reducing further introgression.

Hybrid eradication as a conservation strategy is not without limitations. Eradicating hybrid swarms is much more straightforward than removal of hybrid individuals from a recently invaded population, as the latter scenario will typically require field identification of hybrids. The reliance on morphology for hybrid identification assumes that hybrid phenotypes are intermediate to that of the parental taxa, although this is not always the case (Campton 1987). Furthermore, not all morphological variation has a genetic basis. For example, fishing regulations in the Flathead River drainage define *O. c. lewisi* morphologically by the presence of an orange or red slash on the underside of the throat. However, redband rainbow trout (*Oncorhynchus mykiss gairdneri*) in the adjacent Kootenai River drainage and elsewhere commonly have orange or red throat slashes.

Listing of *O. c. lewisi* under the Endangered Species Act has been controversial, primarily because of dispute over USFWS's morphological, rather than genetic, classification of *O. c. lewisi* and, subsequently, inclusion of hybridized populations as *O. c. lewisi* in the unit considered for listing (USFWS 2003; Campton and Kaeding 2005). For example, USFWS stated that introgressed *O. c. lewisi* with as much as 20% of their genes derived from another taxon would still conform to the morphological taxonomic description of *O. c. lewisi*. Implicit in this argument is the assumption that this amount of admixture would not alter the species in "practical and substantive ways" (USFWS 2003), such as mating behavior or life history. The principal concern over including hybridized populations as *O. c. lewisi* is the threat of protecting sources of future introgression (Allendorf et al. 2004, 2005). The rapid spread of introgression (Hitt et al. 2003) and the pattern of hybrid invasion described in this study indicate that hybrids have different migration behavior than *O. c. lewisi*. Without physical barriers to migration or the eradication of hybrid sources, continued straying and introgression from admixed populations will culminate in the genomic extinction of *O. c. lewisi*. Those remaining nonhybridized *O. c. lewisi* will be restricted to disjunct watersheds above barriers and susceptible to the demographic, environmental, and genetic risks inherent to small populations.

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Trait patterns of aquatic insects across gradients of flow-related factors: a multivariate analysis of Canadian national data

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Abstract: Large-scale comparisons of aquatic bioassessment metrics based on taxonomic composition are currently constrained by the biogeographic limitations of taxon occurrence. The use of species trait patterns offers a possibility to overcome this constraint. We examine the assertion that the trait composition of aquatic insect communities changes in a consistent manner along similar environmental disturbance gradients by evaluating relationships between traits and three flow-related variables (velocity, water temperature, and dissolved oxygen) in 13 independently collected Canadian data sets. Certain trait states such as low crawling rate, common occurrence in drift, short adult life span, erosional rheophily, medium size at maturity, and cold or cool thermal preference were consistently sensitive to all three flow-related factors, velocity in particular, despite biogeographic differences in faunal composition. Trait modalities exhibiting the highest mean correlation with velocity, temperature, and dissolved oxygen were identified, and the potential confounding effect of trait "syndromes" was addressed by restricting the selection of flow-sensitive traits to those with high evolutionary lability. The results of the study provide a basis for the future development of flow bioassessment metrics at the national Canadian scale and potentially at the international scale.

Résumé : La comparaison à grande échelle des métriques de l'évaluation biologique en milieu aquatique basée sur la composition taxonomique est actuellement gênée par les restrictions biogéographiques de la présence des espèces. L'utilisation des patrons de traits biologiques des espèces offre la possibilité de surmonter cette contrainte. Nous examinons l'affirmation selon laquelle la composition des traits biologiques d'une communauté d'insectes aquatiques change de manière semblable le long de gradients similaires de perturbation environnementale en évaluant les relations entre les traits biologiques et trois variables associées au débit (vitesse du courant, température de l'eau et concentration d'oxygène dissous) dans 13 séries de données indépendantes récoltées au Canada. Certains états des traits, tels que taux de reptation faible, présence fréquente dans la dérive, courte durée de la vie adulte, rhéophilie dans la zone d'érosion, taille moyenne à maturité, préférence thermique pour les milieux frais ou froids, sont constamment sensibles à toutes les trois variables reliées au débit, particulièrement à la vitesse de courant, malgré les différences biogéographiques de composition faunistique. Nous avons identifié les modalités des traits qui montrent la corrélation moyenne la plus élevée avec la vitesse, la température et l'oxygène dissous; nous avons corrigé l'effet confondant potentiel des « syndromes » de traits en restreignant notre choix de traits sensibles au débit à ceux qui sont fortement labiles dans l'évolution. Les résultats de notre étude fournissent donc des bases pour l'établissement futur de métriques d'évaluation biologique du débit à l'échelle nationale du Canada et potentiellement pour utilisation internationale.

[Traduit par la Rédaction]

Introduction

Flow, a characteristic physical attribute of stream ecosystems, can be considered as a "master variable" that limits the distribution and abundance of taxa and strongly influences the functional status of river ecosystems (sensu Poff et al. 1997). In the last decade, the development of guidelines for the ecologically sustainable use of river flow has become a priority goal for water management. This need for scientifically defensible guidelines will require significant improvement in our general understanding of the effects of flow alteration on stream biota and, more specifically, in our ability to identify flow-sensitive taxa as a basis for diagnostic tool development.

Stream macroinvertebrates have historically been used as indicators for a variety of human-related impacts, including alterations in flow conditions (Extence et al. 1999; Monk et al. 2006). Although metrics based on changes in community composition of macroinvertebrate communities have been widely adopted, their use is greatly limited by the variability of regional faunas. Specifically, data collected in similar habitat types across biogeographical regions cannot easily be

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combined for assessment of reference condition (sensu Bailey et al. 2004), because different taxa often occupy similar ecological niches in different regions. The use of taxon traits offers a tractable alternative solution to this problem. Traits are characteristics of species that are used to define a biological feature of a taxon or its direct relation to the environment (Poff et al. 2006). The concept of a correspondence between species traits and prevailing environmental factors forms the basis of the habitat template model formulated by Southwood (1977, 1988). The habitat template model predicts that where environmental conditions are similar, taxon trait composition should converge, even across biogeographical boundaries where taxon identities differ.

The trait-based habitat template model has been further developed in relation to the stream fauna into the river habitat templet concept (Townsend and Hildrew 1994) and tested by evaluating the relationships between community trait composition and major environmental gradients (Townsend et al. 1997; Dolédec et al. 1999). The success of the river habitat templet concept stimulated interest in the application of trait-based approaches in biomonitoring. Several studies have demonstrated that by using trait-based approaches, it is possible to discriminate between impacted and reference sites at basin (Charvet et al. 1998), regional (Dolédec et al. 1999), and European scales (Statzner et al. 2001; Gayraud et al. 2003). Employing a trait-based approach to biomonitoring has been most widely advocated in Europe (Usseglio-Polatera et al. 2000; Gayraud et al. 2003; Statzner et al. 2004), and to date, it has found limited application in other parts of the world including North America (e.g., Merritt et al. 2002) and Australia (Chessman and Royal 2004).

The preliminary success of a descriptive trait-based approach in general bioassessment indicates some potential for the development of flow metrics applicable on a large geographical scale (e.g., across Canada). However, there has been little research on the relationship between trait composition and flow within stream macroinvertebrate communities. In streams, flow fluctuations and flow-related factors such as velocity, water temperature, and dissolved oxygen are primary drivers of environmental variability and disturbance, and it is logical to expect that changes in trait composition can be related to changes in flow-related parameters.

Many freshwater macroinvertebrate trait states and modalities have been generated by different authors describing such characters as maximal size, the number of offspring per reproductive cycle, the number of reproductive cycles per individual, life cycle duration of adults, mode of reproduction, existence of parental care, body form, feeding habits, and diet (Gayraud et al. 2003). However, it remains unclear which traits are the best candidates for the development of bioassessment metrics in general and flow-related metrics in particular. Recently, Poff et al. (2006) developed an extensive database of North American aquatic insects with 20 traits (in 59 trait states or modalities) that can be grouped into four categories: life-history, morphological, mobility, and ecological traits. The availability of this unique resource provides an opportunity to design trait-based metrics using a consistent, authoritative, and readily available information base.

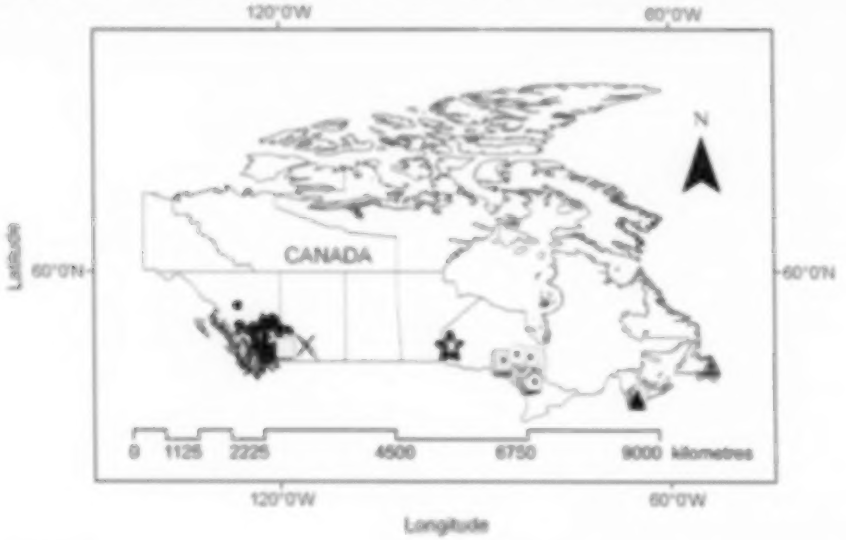
Although a trait-based approach has potential application in the field of bioassessment and biomonitoring, some complications have to be considered that may limit the utility of traits in this context. Some researchers have used traits as independent entities, implying that each trait has, by itself, the potential to provide uniquely valuable information on the structure and functioning of communities (Usseglio-Polatera et al. 2000). However, it has been pointed out that traits often co-evolve and therefore cannot necessarily be treated as independent entities (Poff et al. 2006). The existence of so-called trait "syndromes", i.e., co-adapted trait complexes that may result in individual traits appearing "decoupled" from environmental conditions, has been noticed and widely acknowledged (see Resh et al. 1994; Townsend and Hildrew 1994; Statzner et al. 2004). At the present state of knowledge, it remains unclear whether trait "syndromes" can confound trait-based biological assessment, although the possibility clearly exists.

Here, we aim to answer several questions relating to the environmental occurrence of traits and thus facilitate the development of trait-based flow metrics. Firstly, we examine the assertion that trait composition in aquatic insect communities changes in a similar way along similar environmental disturbance gradients. To do this, we evaluate relationships between taxon traits and three flow-related variables (velocity, water temperature, and dissolved oxygen) in 13 independently collected national and regional Canadian data sets from British Columbia to Newfoundland. Although trait convergence has been demonstrated for fish at a cross-continental scale (Lamouroux et al. 2002) and for macroinvertebrates in streams of the Rocky Mountains (Finn and Poff 2005), it remains to be seen whether the assumption holds for aquatic insects at a continental scale. If trait composition itself and related changes in the representation of each individual trait can be attributed to changes in flow-related variables in a predictable way, despite regional faunal differences, general trait-based metrics could be developed and applied Canada-wide. This could lead to a dramatic reduction in the need for collection of reference data for individual regions and subsequent cost savings that could be redistributed to increase the scope and frequency of assessment and monitoring at a larger number of potentially affected sites.

Our second aim is to identify a suite of traits most responsive to flow-related variables. We recognize that changes in flow regime affect biota through multiple mechanisms, including changes in available habitats, interference with the timing of major life cycle events, and connectivity of populations. Ideally, to evaluate flow-related changes in trait composition, long-term hydrological data should be matched with long-term biomonitoring data. However, such data currently are extremely scarce in Canada. Although we have carried out our analysis with the limited data available, we consider this to be an important step towards the development of more sophisticated hydroecological metrics.

Our third aim is to examine the relationships among traits to identify possible syndromes and, by doing so, suggest an optimum method for applying trait suites as potential ecological indicators of hydrological alteration. Finally, we compare flow-related variables with other potential stressors and natural gradients in terms of explained variability in trait composition.

Fig. 1. Map of the sampling sites in Canada (different studies are indicated by different markers).



Material and methods

The data for this study (Fig. 1) were extracted from the Canadian Aquatic Biomonitoring Information Network (CABIN) online database in October 2006 (cabin.cciw.ca) and comprise 13 independently collected data sets (Table 1). We only used aquatic insects here, because trait information for this group was readily available (Poff et al. 2006). The term "macroinvertebrates" used elsewhere in the text includes aquatic insects plus other groups such as worms and crustaceans and relates to other studies.

Taxonomic level of identification for aquatic insects varied across 13 studies but was available for all at the family level. For this reason, we collated all data at the family level and coded each data set for presence–absence to avoid confounding arising from different collection methods. It has been previously shown that identification at the family level provides descriptions of macroinvertebrate community patterns (Furse et al. 1984; Bournaud et al. 1996; Guerold 2000) similar to those obtained by species identification. Using principal coordinates analysis (PCA) of trait associations between North American aquatic insects, Poff et al. (2006) showed that insect families can be distinguished by applying the same three major trait gradients identified in the analysis of genera. This finding suggests that a substantial amount of variation in trait diversity within benthic communities can be captured by a coarse taxonomic (i.e., family-level) resolution. However, it was noted that the use of family-level data could result in the loss of some potentially important information, especially for the many families that possess a diversity of trait characteristics among the constituent genera (Poff et al. 2006).

Trait compositions for presence–absence data of freshwater macroinvertebrates in Europe showed a similar power to discriminate between different levels of human impact as log-transformed abundances (with raw abundance having less power). Thus, it was concluded that presence–absence data should be sufficient to discriminate functional community changes caused by elevated levels of human impact (Gayraud et al. 2003).

We used the set of 20 traits representing 59 trait states or modalities developed by Poff et al. (2006). These trait states are given for genera grouped by families. In the cases where genera within the same family had different trait modalities, we used modalities for the genera most commonly found in Canada. A total of 53 trait modalities were present in our data. The value of each modality in a sample was calculated as the total number of taxa in a sample possessing this modality. This resulted in a new matrix of 53 modalities × 986 samples, pooling all Canadian studies.

To investigate the convergence of traits across gradients of flow-related factors, we split the trait composition matrix into 13 individual studies and calculated Spearman rank correlation for each modality versus average velocity ($m\cdot s^{-1}$), water temperature (°C), and dissolved oxygen (DO, $mg\cdot L^{-1}$) in each study. The biological data were collected from a range of different streams with different ranges of velocity, temperature, and DO; thus the correlation values themselves were not as informative as a rank of relationship strengths between each trait modality and flow-related factors. For this reason, we range-standardized correlation values by trait to make them more comparable and demonstrated variability in correlation values using box plots. Range standardization was performed using following formula:

$$x' = [x - \min(x)] / [\max(x) - \min(x)]$$

All resulting values were between 1 (the highest correlation) and 0 (the lowest correlation). Twenty modalities with the highest mean correlations were identified as potential indicators for changes in flow.

To answer a question of whether there was evidence of a strong geographical pattern within the trait composition matrix, we conducted PCA. To evaluate variability in the trait composition matrix explained by flow-related variables in

Table 1. Description of the 13 data sets employed in this study.

Study	Year	Province	No. of samples
Fraser River	1994–2004	British Columbia	468
Federal–provincial water quality monitoring stations	2003–2004	British Columbia	28
GVRD CABIN–BIBI comparison	2004	British Columbia	58
Streambank stabilization project	2005	British Columbia	23
Vancouver Island	2001	British Columbia	31
EEM Fraser 98	1998	British Columbia	20
Hemlo reference streams	2003–2004	Ontario	36
Moose River 1999	1999	Ontario	77
Red Lake streams	2003	Ontario	25
Sudbury streams	2003–2005	Ontario	107
Annapolis River	2002–2004	Nova Scotia	21
Kejimkujik National Park	2002, 2005	Nova Scotia	46
Terra Nova National Park CABIN	2002–2003	Newfoundland and Labrador	20

Note: All data are currently housed in Environment Canada's CABIN database.

comparison with some major potential stressors and natural gradients, we applied redundancy analysis (RDA) to the combined trait composition matrix (53 trait modalities, with each modality expressed as the number of taxa possessing this modality in a sample, × 986 samples) using CANOCO 4.53 software (Biometris – Plant Research International, Wageningen, the Netherlands). The following environmental variables were employed: electrical conductivity of water (EC, $\mu S \cdot cm^{-1}$), altitude (m), total phosphorus (TP, $mg \cdot L^{-1}$), total Kjeldahl nitrogen (TKN, $mg \cdot L^{-1}$), pH, total suspended sediments (TSS, $mg \cdot L^{-1}$), and stream order (1–8). We used RDA because of the extremely short gradient in trait matrix as identified by detrended correspondence analysis (1.08) and because we were particularly interested in quantitative changes in individual modalities in addition to overall changes in trait composition. We applied a step-forward selection procedure to identify the relative contribution of each variable in relation to the overall variance explained and tested the significance of each variable by using 499 Monte Carlo permutations. For comparison, we applied RDA to the taxonomic matrix (the presence–absence of 51 aquatic insect families used for the derivation of the trait matrix) using the same set of environmental variables. To address the issue of trait syndromes, we used cluster analysis, employing a group-average linkage dendrogram based on Bray–Curtis similarity (PRIMER 5.2 software; Primer-E Ltd., Ivybridge, UK). Cluster analysis was applied to the trait matrix only (53 trait modalities × 986 samples).

Results

Abbreviations and full definitions for all traits and trait modalities used in this study are provided (Table 2), as well as mean standardized correlations, standard deviations, and proportions of significant correlations between each trait modality and flow-related variables across all 13 studies.

Trait convergence across gradients of flow-related factors

When we considered correlations between each trait modality and flow-related factors separately in each of 13 studies, there was close correspondence among the different studies used in the analysis between trait modalities and velocity in particular. This is illustrated by box plots showing the median and range of values across all studies (Fig. 2). There was less agreement among the different studies on the relationships between traits, temperature, and DO (Fig. 2); however, it was still evident that certain traits such as cold and cool thermal preference and medium size at maturity had consistently high correlation with DO and negative correlation with water temperature.

To demonstrate whether specific traits were sensitive to all three factors (velocity, temperature, and DO) across all studies, we selected 20 trait modalities with the highest sensitivity to each of the flow-related variables based on their mean standardized correlations (these more sensitive traits are indicated in Table 2 by shading). Many of the traits sensitive to velocity are also sensitive to temperature and DO (e.g., armoring: none, common occurrence in drift, weak adult flying strength, short adult life span).

General patterns in combined trait matrix

The results of the PCA on the combined data matrix are shown (Fig. 3) to demonstrate if there was evidence of a strong geographical pattern within the trait composition matrix (sample sites are marked by province). The PCA identified a major gradient along the first axis, with an eigenvalue of 0.79; the eigenvalues for three subsequent axes were much lower (0.07, 0.03, and 0.02, respectively). Although there was some separation between data from British Columbia and those from the other provinces along the second axis, the first, major axis gradient fails to reveal significant spatial heterogeneity.

RDA with 10 variables (Fig. 4, only selected variables are shown) explained 12.7% of variability in the combined trait matrix. All four axes extracted were significant, with the first axis having a higher eigenvalue (0.1) than three subsequent ones (0.02, 0.004, and 0.003, respectively). A step-forward selection procedure identified velocity as the variable with greatest explanatory power (from those available) for both marginal effects, using individual environmental variables separately in the order of variance explained (lambda 1), and conditional effects, using environmental variables in order of

Table 2. Definitions, abbreviations, mean standardized correlations, standard deviations (SD), and proportions of statistically significant (PrSig) at <0.05 correlations between trait modalities and flow-related variables across all 13 studies.

			Velocity			Water temperature			Dissolved oxygen		
Trait	Trait state (modality)	Code	Mean	SD	PrSig	Mean	SD	PrSig	Mean	SD	PrSig
Armoring	Poor (heavily sclerotized)	ArmPoor	0.63	0.19	0.38	0.56	0.21	0.23	0.48	0.15	0.09
Armoring	Good (e.g., some cased caddisflies)	ArmrGood	0.43	0.23	0.15	0.53	0.24	0.15	0.41	0.22	0.09
Armoring	None (soft-bodied forms)	ArmrNone	0.77	0.13	0.54	0.45	0.20	0.23	0.67	0.19	0.18
Attachment	Both	AtchBoth	0.50	0.23	0.23	0.62	0.22	0.23	0.39	0.28	0.09
Attachment	Free-ranging	AtchFRge	0.67	0.19	0.46	0.51	0.21	0.23	0.64	0.15	0.09
Attachment	Sessile, sedentary	AtchSSed	0.82	0.12	0.69	0.52	0.20	0.23	0.51	0.22	0.09
Maximum crawling rate	High (>100 cm·h^{-1})	CrwlHigh	0.52	0.14	0.23	0.43	0.23	0.15	0.63	0.22	0.27
Maximum crawling rate	Low (<100 cm·h^{-1})	CrwlLow	0.80	0.18	0.54	0.51	0.21	0.23	0.64	0.21	0.18
Maximum crawling rate	Very low (<10 cm·h^{-1})	CrwlVLow	0.59	0.19	0.38	0.55	0.23	0.15	0.40	0.15	0.09
Ability to survive desiccation	Absent	DesiNo	0.74	0.16	0.46	0.59	0.21	0.31	0.57	0.19	0.27
Development	Fast seasonal	DevFSeas	0.57	0.14	0.23	0.50	0.23	0.31	0.55	0.24	0.09
Development	Nonseasonal	DevNSeas	0.52	0.18	0.15	0.57	0.26	0.15	0.24	0.20	0.09
Development	Slow seasonal	DevSSeas	0.77	0.14	0.54	0.56	0.20	0.31	0.60	0.14	0.09
Female dispersal	Low (<1 km flight before laying eggs)	DispLow	0.73	0.15	0.54	0.45	0.21	0.23	0.63	0.16	0.18
Occurrence in drift	Abundant (dominant in drift samples)	DrftAbnd	0.52	0.34	0.23	0.60	0.29	0.00	0.55	0.35	0.09
Occurrence in drift	Common (typically observed)	DrftComn	0.77	0.13	0.46	0.48	0.20	0.23	0.61	0.21	0.27
Occurrence in drift	Rare (catastrophic only)	DrftRare	0.71	0.16	0.46	0.52	0.22	0.23	0.59	0.12	0.09
Adult ability to exit	Absent (not including emergence)	ExitNo	0.76	0.13	0.62	0.49	0.22	0.23	0.61	0.14	0.18
Adult flying strength	Weak (e.g., cannot fly into light breeze)	FlgtWeak	0.74	0.13	0.54	0.49	0.22	0.23	0.63	0.17	0.18
Habitat	Burrow	HabBurrw	0.36	0.17	0.23	0.60	0.31	0.08	0.44	0.27	0.18
Habitat	Climb	HabClimb	0.47	0.28	0.31	0.44	0.31	0.31	0.44	0.18	0.18
Habitat	Cling	HabCling	0.83	0.16	0.62	0.56	0.24	0.31	0.57	0.19	0.09
Habitat	Sprawl	HabSprwl	0.63	0.19	0.15	0.38	0.24	0.15	0.56	0.24	0.09
Habitat	Swim	HabSwim	0.45	0.16	0.31	0.55	0.26	0.31	0.60	0.25	0.36
Adult life span	Long (>1 month)	LifeLong	0.44	0.16	0.08	0.65	0.26	0.31	0.32	0.28	0.27
Adult life span	Short (<1 month)	LifeShrt	0.76	0.15	0.62	0.48	0.17	0.23	0.61	0.16	0.18
Adult life span	Very short (<1 week)	LifeVShrt	0.66	0.20	0.54	0.55	0.21	0.31	0.58	0.23	0.18
Respiration	Plastron, spiracle (aerial)	RespAir	0.14	0.17	0.38	0.50	0.35	0.23	0.38	0.33	0.18
Respiration	Gills	RespGills	0.75	0.19	0.46	0.65	0.23	0.38	0.59	0.22	0.18
Respiration	Tegument	RespTeg	0.70	0.23	0.46	0.32	0.21	0.23	0.60	0.24	0.09
Rheophily	Depositional and erosional	RheoBoth	0.75	0.15	0.54	0.54	0.24	0.23	0.59	0.15	0.18
Rheophily	Depositional only	RheoDep	0.17	0.15	0.31	0.55	0.28	0.08	0.36	0.26	0.18
Rheophily	Erosional	RheoEr	0.81	0.16	0.54	0.49	0.18	0.23	0.56	0.19	0.09
Shape	Streamlined (flat, fusiform)	ShpeStrL	0.64	0.18	0.31	0.61	0.24	0.46	0.59	0.28	0.27
Size at maturity	Large (>16 mm)	SizeLrge	0.64	0.23	0.46	0.51	0.22	0.31	0.52	0.16	0.09
Size at maturity	Medium (9–16 mm)	SizeMed	0.82	0.11	0.54	0.45	0.19	0.23	0.68	0.15	0.27
Size at maturity	Small (<9 mm)	SizeSmal	0.59	0.20	0.38	0.56	0.23	0.31	0.47	0.17	0.09
Swimming ability	None	SwimNone	0.72	0.19	0.46	0.55	0.22	0.23	0.49	0.23	0.18
Swimming ability	Strong	SwimStro	0.45	0.15	0.15	0.56	0.22	0.31	0.59	0.21	0.27
Swimming ability	Weak	SwimWeak	0.73	0.31	0.69	0.45	0.33	0.31	0.66	0.17	0.18
Synchronization of emergence	Poorly synchronized (weeks)	SyncPWks	0.44	0.21	0.23	0.64	0.24	0.38	0.43	0.24	0.27

Table 2 *(concluded).*

Trait	Trait state (modality)	Code	Velocity			Water temperature			Dissolved oxygen		
			Mean	SD	PrSig	Mean	SD	PrSig	Mean	SD	PrSig
Thermal	Cold stenothermal or cool eurythermal	TheCldSt	0.76	0.24	0.62	0.37	0.31	0.38	0.76	0.15	0.09
Thermal	Cool–warm eurythermal	TheCoolW	0.70	0.14	0.54	0.63	0.17	0.23	0.50	0.24	0.18
Thermal	Warm eurythermal	TheWarm	0.34	0.11	0.00	0.73	0.05	0.00	0.60	0.11	0.00
Feeding habits	Collector–filterer	TrColFilt	0.59	0.17	0.31	0.65	0.21	0.23	0.58	0.29	0.27
Feeding habits	Collector–gatherer	TrColGth	0.77	0.20	0.46	0.50	0.21	0.15	0.50	0.19	0.18
Feeding habits	Herbivore (scraper, piercer, and shedder)	TrHerb	0.72	0.18	0.54	0.48	0.29	0.31	0.63	0.20	0.27
Feeding habits	Predator (piercer and engulfer)	TrPred	0.60	0.19	0.38	0.48	0.25	0.31	0.47	0.19	0.09
Feeding habits	Shredder (detritivore)	TrShred	0.62	0.15	0.38	0.31	0.22	0.23	0.66	0.27	0.18
Voltinism	Bi- or multi-voltine (>1 generation·year)	VoltBiMu	0.63	0.17	0.31	0.52	0.17	0.08	0.45	0.28	0.09
Voltinism	Semivoltine (<1 generation·year)	VoltSemi	0.66	0.15	0.54	0.60	0.21	0.08	0.52	0.24	0.18
Voltinism	Univoltine (1 generation·year)	VoltUni	0.67	0.20	0.46	0.56	0.22	0.31	0.60	0.16	0.18

Note: Relatively high mean standardized correlations are shaded for comparison.

their inclusion in the model, together with the additional variance each variable explained at the time of inclusion (lambda A) (Table 3). All variables except TKN were significant ($p < 0.05$, identified by Monte Carlo permutation test), with EC and altitude explaining the largest amount of variability after velocity. RDA applied to the taxonomic matrix produced very similar results. Ten variables explained 14% of all variability in the taxonomic matrix, with altitude and velocity having the greatest explanatory power.

Trait "syndromes" investigated by cluster analysis

A dendrogram of Bray–Curtis similarities between individual trait states (Fig. 5) shows that many potentially flow-sensitive trait modalities (armoring: none, weak adult flying strength, adult ability to exit: absent, low female dispersal, habitat: cling, weak swimming ability, cold and cool thermal preference) are present in group 1. In fact, all trait modalities in group 1 (with the exception of "very short adult lifespan") are identified within the top 20 traits sensitive to one or more flow-related variables. Group 2 also includes mostly traits with high to medium sensitivity to one or more flow-related variables (rheophily: erosional, attachment: sessile). Trait modalities "very low crawling rate" and "poor armoring" are not in the list of top 20 sensitive variables; however, by definition, they are more similar to flow-sensitive modalities "low crawling rate" and "armoring: none" than to tolerant modalities "high crawling rate" and "armoring: good". Trait modalities with high tolerance to flow-related variables were mainly clustered together in group 3. In this group, only "high crawling rate" was classified as sensitive to temperature and DO but not to velocity.

Discussion

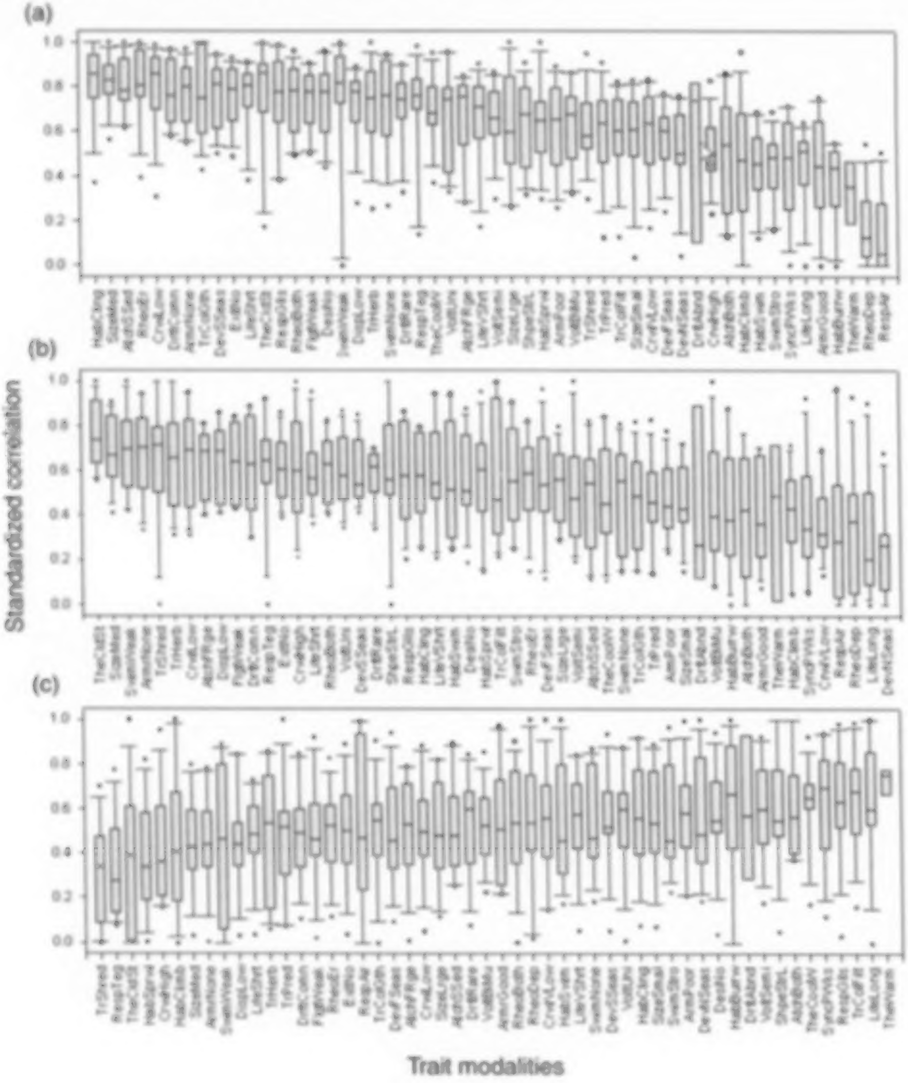
Trait convergence across gradients of flow-related factors

Using data collected in 13 independent studies across Canada, we have shown that certain species traits correlate with average stream velocity in a consistent way, irrespective of their geographic origins. Although the majority of samples were collected in British Columbia (mountainous terrain with fast-flowing rivers), all 13 data sets were equally weighted in the correlation analysis. Thus, with less than half of the studies (6 out of 13) originating from British Columbia, we are confident that we have minimized the geographical bias in our analysis.

Similar results were previously shown for fish from two different continents (Lamouroux et al. 2002) and for macroinvertebrates from four physically similar Rocky Mountain streams (Finn and Poff 2005); however, to our knowledge, ours is the first study involving aquatic insects at a cross-continental scale. Trait modalities highly correlated with velocity responded consistently across studies, and in addition, patterns of trait composition across gradients of water temperature and dissolved oxygen were also evident. Based on our results, we suggest that traits appear to be globally responsive to environmental drivers and that the trait-based approach has great potential for application in the design of biomonitoring metrics with widespread applicability, even outside their geographical regions of origin.

We suggest that the traits most sensitive to velocity should be the primary candidates for the flow bioassessment met-

Fig. 2. Box plots showing the range of standardized correlation values between each trait modalitity and flow-related factors ((*a*) velocity, (*b*) dissolved oxygen, and (*c*) water temperature) in 13 independent studies.



rics. Though we recognize that velocity is only one of the multitude of factors affected by changes in flow regime, velocity-based metrics such as the UK LIFE index (Extence et al. 1999) have shown strong relationships with hydrological parameters such as magnitude of flow (Monk et al. 2006). In addition, the RDA on the combined trait matrix demonstrated that velocity explained the greatest proportion of the variability within the data and was highly significant. Thus, we propose that a suite of velocity-sensitive trait modalities can be used as a basis for the development of flow metrics, which can be further refined as more information on the relationships between community trait composition and descriptors of the flow regime become available.

Analysis of changes in trait composition with changes in temperature and DO added little explanatory power to the direct relationship with velocity. Most of the trait states sensitive to velocity were also sensitive to temperature and (or) DO (armoring: none, slow seasonal development, low female dispersal, common occurrence in drift, adult ability to exit: absent, weak adult flying strength, short adult life span, rheophily: both, rheophily: erosional, medium size at maturity, weak swimming ability, cold and cool thermal preference, collector–gatherer, herbivore). This is not surprising, as temperature, dissolved oxygen, and velocity are often correlated. For example, in the data set used for this study, Pearson *r* between DO and temperature was –0.52 ($p < 0.05$,

Fig. 3. Principal component analysis (PCA) on combined trait modalities matrix with sites marked by provinces (circles, Nova Scotia; triangles, Ontario; crosses, Newfoundland and Labrador; squares, British Columbia).

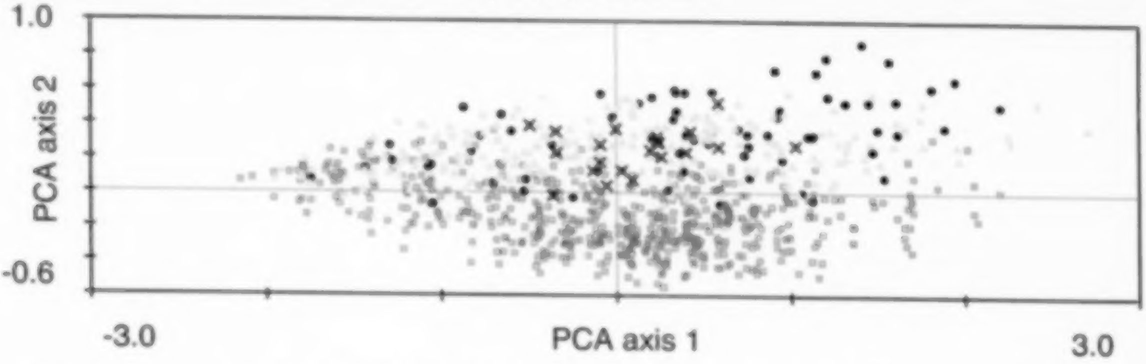
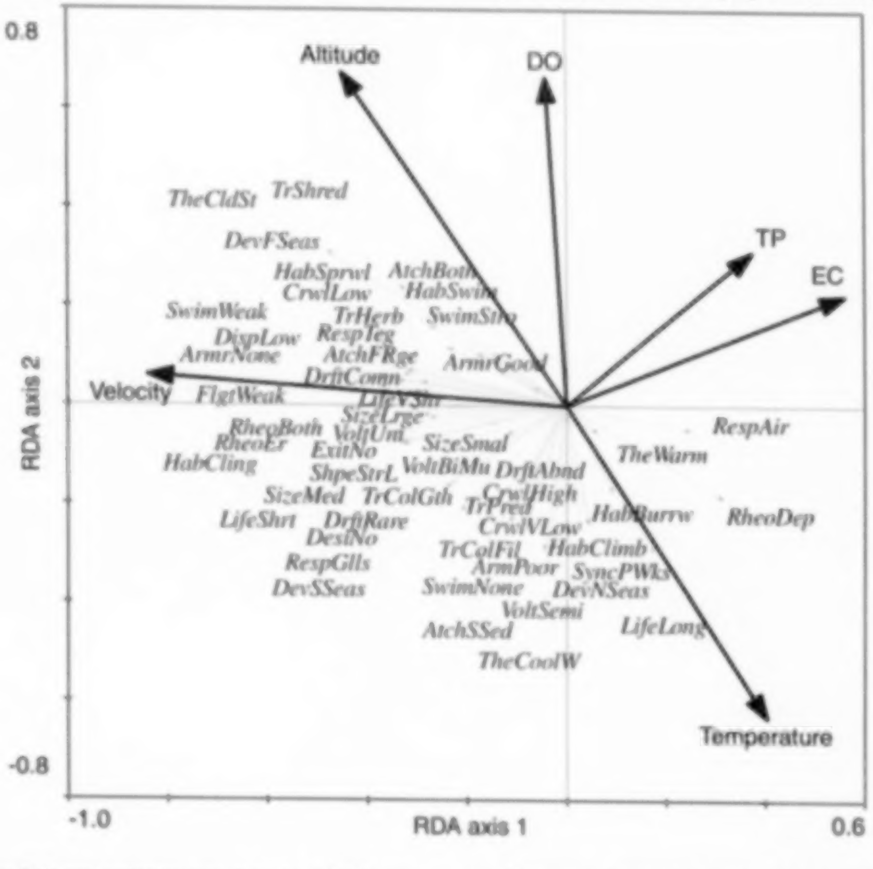


Fig. 4. Redundancy analysis (RDA) with selected variables (all studies together, trait labels have been slightly moved to improve readability).



$n = 854$), between DO and velocity was 0.41 ($p < 0.05$, $n = 854$), and between temperature and velocity was –0.37 ($p < 0.05$, $n = 854$).

Trait syndromes investigated by cluster analysis

Cluster analysis has shown that most of the velocity-sensitive trait states were indeed linked, demonstrating the potential influence of trait syndromes as confounding factors. However, it remains unclear whether these linkages are a result of an existing trait syndrome or simply that those traits are externally constrained to respond similarly to the same gradient. If trait syndromes were confounding the assessment, we would expect to see trait modalities mechanistically unrelated to flow appearing sensitive to velocity merely by association with other sensitive traits for which we can see a clear mechanistic explanation for the response.

Fig. 5. Cluster analysis of Bray–Curtis similarities between individual trait modalities (each modality represents a count of taxa possessing this modality) in the combined data matrix from all 13 studies.

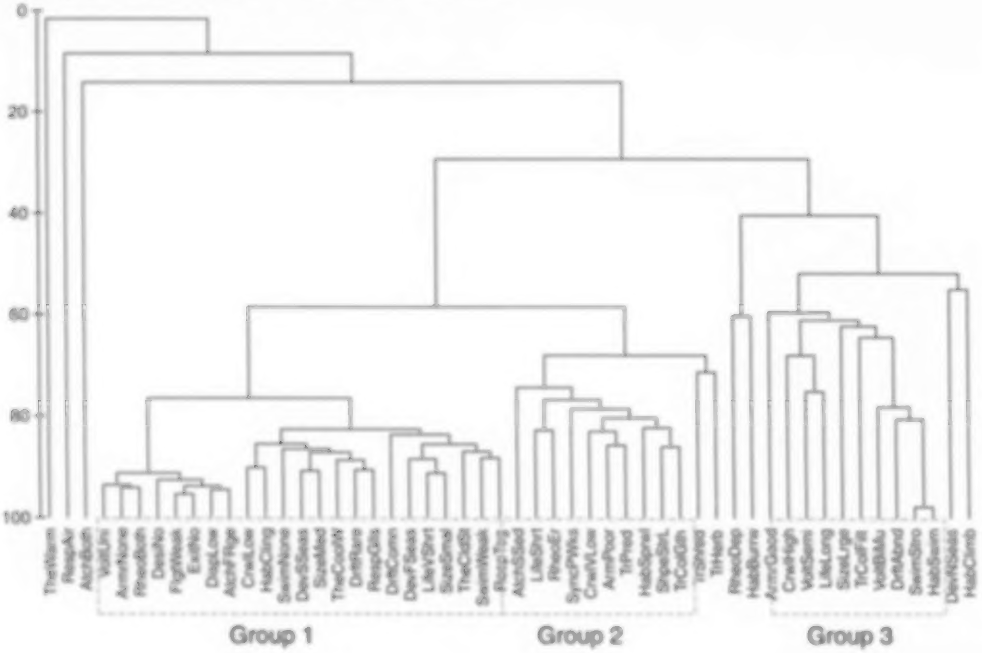


Table 3. Results of the redundancy analysis (RDA) step forward-selection procedure (all 13 data sets pooled together, 986 samples).

Marginal effects		Conditional effects		
Variable	Lambda 1	Variable	Lambda A	*p*
Velocity	0.06	Velocity	0.06	0.002
EC	0.03	EC	0.02	0.002
Altitude	0.03	Altitude	0.01	0.002
Temperature	0.02	TSS	0.01	0.002
TP	0.01	pH	0.01	0.006
DO	0.01	Temperature	0.01	0.004
pH	0.01	Stream order	0.00	0.008
TSS	0.01	DO	0.01	0.014
TKN	0.01	TP	0.00	0.012
Stream order	0.00	TKN	0.00	0.212

Note: Marginal effects indicate variance explained (lambda 1) by individual environmental variables separately and conditional effects (lambda A) using environmental variables in order of their inclusion in the model, together with the additional variance of each variable explained at the time of inclusion. EC, electrical conductivity of water; TP, total phosphorus; DO, dissolved oxygen; TSS, total suspended sediments; TKN, total Kjeldahl nitrogen.

For example, many species in orders Ephemeroptera and Plecoptera are known to have high velocity preferences (Extence et al. 1999); thus, we would expect an increase in occurrence of these orders with an increase in velocity. The trait syndrome for these orders is "armoring: none", "fast seasonal development", "very short adult life span", and "small size at maturity" (Poff et al. 2006). Indeed, these traits were grouped in the cluster analysis, with "armoring: none" and "small size at maturity" identified as sensitive to flow velocity. However, two other traits (fast seasonal development and very short adult life span) were only moderately sensitive to velocity. Similarly, if we consider trait syndrome characteristics for the Trichoptera, Diptera, and Coleoptera identified by Poff et al. (2006) (swimming ability: none, attachment: sessile, rheophily: erosional, armoring: good, and short adult life span), all these traits but "armoring: good" belong to the same large cluster and are sensitive to velocity. Thus, we see that traits identified as phylogenetically related parts of a trait syndrome generally tend to co-occur, but they also tend to have similar sensitivity. As a possible solution to the potential problem of trait syndromes, Poff et al. (2006) have suggested using phylogenetically independent traits (e.g., those showing high evolutionary lability) such as voltinism, occurrence in drift, temperature preferences, feeding guild, rheophily, crawling rate, and size at maturity. Phylogenetically independent or labile traits are responsive to local selection; therefore, similarity among taxa with respect to these traits will be largely independent of their phylogenetic relationships (sensu Poff et al. 2006). In our case, voltinism did not appear to be highly sensitive to velocity; however, trait "univoltine" belongs to group 1 and is linked with several other flow-sensitive trait states, thus it might be recommended as a potential indicator trait modality. The rest of the traits suggested by Poff et al. (2006) contain one or more modalities sensitive to velocity. We suggest use of the following traits as potential flow indicators: low crawling rate, common in drift, short adult lifespan, rheophily: erosional, medium size at maturity, and cold and cool thermal preference. Several other traits could be considered as good candidates, shown to be sensitive to velocity (e.g., weak swimming ability, swimming ability: none, respiration: gills, habitat: cling, weak adult flying strength, adult ability to exit: none, low female dispersal, slow seasonal development, ability to survive desiccation: absent, attachment: sessile, and armoring: none); however, according to Poff et al. (2006), they can be evolutionarily linked to other traits through a trait syndrome and should be used with caution. Even though feeding habit trait modalities "collector–gatherer" and "herbivore" appear to be sensitive to velocity, we advise caution when using these traits as they might be strongly influenced by a variety of other factors (e.g., nutrients).

Application in biomonitoring and future research needs

The results of our multivariate RDA suggest that even though velocity has a strong influence on trait composition, other factors such as EC and altitude have a significant effect also. Finn and Poff (2005) have shown that the river continuum concept applies to traits in a similar way as to taxonomic composition. Therefore, we suggest the following application of trait metrics in flow bioassessment: typical ranges in count or proportion of flow-sensitive traits should be identified for reference streams with different hydrological regimes (e.g., snow-fed, rainfall-fed, permanent, intermittent), different sizes, orders, and slopes. These reference ranges could be used as bioassessment metrics at a global scale (i.e., beyond the confines of biogeographic regions) for a wide variety of stream types.

Even though the trait-based approach has a clear potential for the biomonitoring, there are a number of questions that remain to be addressed. In comparison with the traditional taxon-based approach in which sensitive taxa are well known and metrics are well established and widely tested, there have been few practical studies linking traits with environmental gradients. There is still a diversity of opinions on the ways to describe and quantify traits, and the need for the unified approach allowing for comparisons on a wide geographical scale is evident. In this study we used a recently compiled database of traits for North American aquatic insects; however, this database is not exhaustive and many other traits could be identified and potentially used for bioassessment purposes. For example, Usseglio-Polatera et al. (2000) have identified other useful traits such as reproduction with states like ovoviviparity, isolated eggs, clutches, asexual reproduction, dispersal (aquatic passive, aquatic active, aerial active, aerial passive), and resistance form (eggs, cocoons, diapause or dormancy). Given the multitude of factors affecting aquatic insects communities in streams, some overlap among traits sensitive to velocity and other factors (e.g., nutrients) is likely. Increasing the number of traits could provide better discriminatory power in examining multiple stressor situations. Discrimination between different types of impact will be a key focus for future research. In this respect it would be beneficial to extend the trait approach beyond aquatic insects to include all stream macroinvertebrates, in addition to expanding the number of traits and trait modalities.

We suggest that future research on the development of flow-related metrics should be focused on relationships between flow regime descriptors and trait composition. Biologically relevant descriptors of flow regime have been identified by Richter et al. (1996) and include 32 parameters, organized into five groups (magnitude of monthly water conditions, magnitude and duration of annual extreme water conditions, timing of annual extreme water conditions, frequency and duration of high and low pulses, and rate and frequency of water condition changes). Provided that relevant hydrological and biological data are available, these parameters could be linked to the trait matrix in relation to velocity, temperature, and DO, and sensitive trait modalities could be identified.

Although the data employed in this study reflect the single largest biomonitoring data set available for Canada, the data still reflect regional bias in faunistic composition (e.g., overrepresentation of the British Columbia fauna, underrepresentation of the Prairie fauna and Canadian Shield fauna). However, the generic approach developed here, employing generic traits rather than geographically constrained taxonomic units, offers the potential for these data to be used in formulating more general statements for testing in future studies. Clearly, as our national network grows, we envisage the potential to update our analyses to correct any bias inherent in the underrepresentation of regional faunas.

In conclusion, we have demonstrated that the trait approach can be used to develop new flow bioassessment metrics, as the representativeness of certain trait modalities and overall trait composition shows a similar relationship with velocity irrespective of geographic origin. Using a national data set representing a continental scale, we have identified trait modalities exhibiting the highest mean correlation with velocity, temperature, and DO and have addressed the potential confounding effect of trait syndromes by following the advice of Poff et al. (2006) and restricting the selection of traits to those with high evolutionary lability, less correlated with other traits. The results of our study provide a basis for the future development of flow bioassessment metrics at the national Canadian scale.

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Seasonal variations in stable isotope ratios of juvenile coho salmon (*Oncorhynchus kisutch*) from western Washington rivers

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Abstract: Salmon carcasses provide a marine derived nutrient (MDN) subsidy to river systems, but the extent to which it affects juvenile salmon growth is unclear. To evaluate temporal and spatial nutrient contributions from watershed sources and MDNs using stable isotopes, Skagit River (Washington, USA) juvenile coho salmon (*Oncorhynchus kisutch*) were collected. Muscle samples were taken from fry through smolts to measure temporal changes in $\delta^{15}N$ and $\delta^{13}C$. $\delta^{15}N$ and $\delta^{13}C$ levels declined from emergence until fall, when they approached values for resident cutthroat trout (*Oncorhynchus clarkii*) collected above anadromous barriers. Muscle $\delta^{13}C$ was highly variable and did not increase subsequently. However, coho salmon $\delta^{15}N$ increased during the winter. March coho salmon parr $\delta^{15}N$ levels suggested high variability in carcass availability for consumption. During the next spring, $\delta^{15}N$ levels again declined. In Griffin Creek, a Snoqualmie River tributary, a significant relationship between carcass density and $\delta^{15}N$ and $\delta^{13}C$ levels was found in March coho salmon parr. At high spawner densities, some parr $\delta^{15}N$ exceeded carcass values; however, parr $\delta^{13}C$ increased moderately. These findings show that stable isotope data provide insights on seasonal sources of nutrients. In addition, results indicate that March coho salmon parr $\delta^{15}N$ levels would be a useful index of carcass availability for overwintering juvenile consumption.

Résumé : Les carcasses de saumons représentent une allocation de nutriments d'origine marine (MDN) aux systèmes fluviaux; il n'est cependant pas clair dans quelle mesure cet apport affecte la croissance des jeunes saumons. Nous avons prélevé de jeunes saumons coho (*Oncorhynchus kisutch*) dans la Skagit (Washington, É.-U.) afin d'évaluer à l'aide d'isotopes stables les contributions temporelles et spatiales provenant des sources du bassin versant et des MDN. Des analyses d'échantillons de muscle des divers stades, des alevins aux saumoneaux, ont permis de mesurer les changements temporels de $\delta^{15}N$ et de $\delta^{13}C$. Les valeurs de $\delta^{15}N$ et de $\delta^{13}C$ diminuent de l'émergence jusqu'en automne au moment où elles s'approchent des valeurs observées chez les truites fardées (*Oncorhynchus clarkii*) récoltées en amont des barrières pour la migration anadrome. Les valeurs de $\delta^{13}C$ du muscle sont très variables et n'augmentent pas par la suite. En revanche, les valeurs de $\delta^{15}N$ du saumon coho croissent pendant l'hiver. Les valeurs de $\delta^{15}N$ des tacons en mars indiquent une grande variabilité dans la disponibilité des carcasses à consommer. Au printemps suivant, les valeurs de $\delta^{15}N$ déclinent à nouveau. Dans Griffin Creek, un tributaire de la Snoqualmie, il existe une relation significative entre la densité des carcasses et les valeurs de $\delta^{15}N$ et de $\delta^{13}C$ mesurées chez les tacons de saumons coho en mars. Aux fortes densités de reproducteurs, les valeurs de $\delta^{15}N$ de certains tacons surpassent celles des carcasses. Par ailleurs, les valeurs de $\delta^{13}C$ des tacons augmentent modérément. Ces observations montrent que les mesures des isotopes stables fournissent des informations sur les sources de nutriments au cours des saisons. De plus, nos résultats indiquent que les valeurs de $\delta^{15}N$ chez les tacons des saumons coho en mars pourraient servir d'indice commode de la disponibilité des carcasses à consommer par les jeunes au cours de l'hiver.

[Traduit par la Rédaction]

Introduction

The marine phase of the salmon life cycle is responsible for greater than 99% of adult body mass (Welch and Parsons 1993), and carcasses can provide a substantial subsidy of marine-derived nutrients (MDNs) to their natal streams (Gende et al. 2004). Carcasses and eggs are a high-quality food source containing elevated levels of lipids and proteins that stream-rearing fish such as juvenile coho salmon (*Oncorhynchus kisutch*) consume (Bilby et al. 1998; Mathisen et al. 1998). In addition, MDNs are also cycled from carcasses into stream invertebrate communities and then to juvenile coho salmon (Kline et al. 1990; Bilby et al. 1996).

Stable isotope ratio analysis is a useful tool for assessing relative contributions of MDNs to the various compartments

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of stream and riparian communities (Bilby et al. 1996, 2003; Wipfli et al. 1998). The relationship of isotopes ^{15}N to ^{14}N, known as δ^{15}N, is elevated in adult salmon tissue relative to the streams where they spawn. δ^{15}N can be used as a tracer to estimate the relative contribution of nitrogen from MDNs to nitrogen budgets of stream flora and fauna (Bilby et al. 1996; Reimchen 2001). For example, Bilby et al. (1998) showed that condition factors for juvenile steelhead and coho salmon increased in the presence of salmon carcasses, and stable isotope signals in muscle indicated that the proportion of marine-derived nitrogen in muscle tissue was as much as 39% after carcass placement. Additional research indicated that higher δ^{15}N values in juvenile salmonids were associated with density of carcasses (Bilby et al. 2001). Likewise, in a southeastern Alaska stream, Wipfli et al. (2003) showed that coho salmon, cutthroat trout (*Oncorhynchus clarkii*), and dolly varden (*Salvelinus malma*) grew significantly faster when salmon carcasses were present, and they retained their body mass into the following spring. Other studies have used stable isotope analysis to provide information on the extent of MDN dispersal into surrounding riparian communities (Reimchen 2001; Bilby et al. 2003).

At present, stable isotope studies have looked at isolated time points during the freshwater phase of juvenile coho salmon, and the results are insufficient to accurately portray the influence of MDNs over this time period. In this study, we followed δ^{15}N and δ^{13}C levels in juvenile coho salmon throughout the freshwater growth period in the Skagit River basin to evaluate seasonal inputs of nitrogen and carbon from salmon and other sources. We also examined δ^{15}N levels from fish rearing in an 20 additional basins in the Puget Sound and Washington coast regions to verify whether samples collected across watersheds without controlling for time would match the longitudinal patterns found in the Skagit River. Finally, we examined how δ^{15}N and δ^{13}C signals varied with density of spawners in Griffin Creek, a tributary of the Snoqualmie River.

Materials and methods

Seasonal variation of δ^{15}N and δ^{13}C in juvenile coho

Wild juvenile coho salmon (122 fish) were collected weekly (March to July 2004 and February to July 2005) at the Washington Department of Fish and Wildlife (WDF&W) Skagit River smolt trap at Mount Vernon, Washington, and by seine from Finney Creek, a Skagit River tributary, in July and October 2004. We checked all fish for fin erosion or hatchery fin clips and none was detected, indicating that the fish were wild. Samples were stored at –20 °C until processing. Fork length and whole-body wet weight measurements were taken. In addition, native cutthroat trout (ages 0+ and 1+; $n = 12$) were collected from Skagit River tributaries (Ennis, Hilt, Mouse, and Parker creeks) by electroshocking above impassable barriers. Fork length of the cutthroat was measured, and weight was estimated using a regression analysis ($n = 340$, $r^2 = 0.99$, $p < 0.01$) of cutthroat weight versus length data. The stream sections where reference cutthroat trout were collected are above possible nitrogen inputs from dairy farms and sewage discharge that could potentially affect δ^{15}N values. Cutthroat trout tissue was used to provide background δ^{15}N and δ^{13}C tissue values that would be generated in the absence of salmon carcasses (some δ^{15}N data are from Bilby et al. 2001).

We used a growth-dependent model to estimate N isotope trends in juvenile Skagit coho salmon after emergence, assuming that the coho salmon diet had the same δ^{15}N values as the reference cutthroat trout diet. It was assumed that isotopic turnover was due only to tissue growth and the influence of metabolism was negligible (Herzka and Holt 2000; Perry et al. 2003). This trend was calculated using the following equation:

$$(1)\quad \text{Muscle } \delta^{15}\text{N} = [(\delta^{15}\text{N}_0)\text{wt}_0 + \delta^{15}\text{N}_\text{C}(\text{wt}_\text{F} - \text{wt}_0)]\cdot \text{wt}_\text{F}^{-1}$$

where $\delta^{15}\text{N}_0$ is the initial fry δ^{15}N value, wt_0 is the initial weight, $\delta^{15}\text{N}_\text{C}$ is the average δ^{15}N for resident cutthroat trout collected from four Skagit River tributaries above impassable barriers, and wt_F is the weight at sampling.

In addition to Skagit River samples, juvenile coho salmon (ages 0+ and 1+; 132 fish) were also collected at various times (March through September 1996, 1997, 1999, 2000, 2001, and 2002) by electroshocking at sites in western Washington (Fig. 1), and some of the data shown in Fig. 4 are from Bilby et al. (2001).

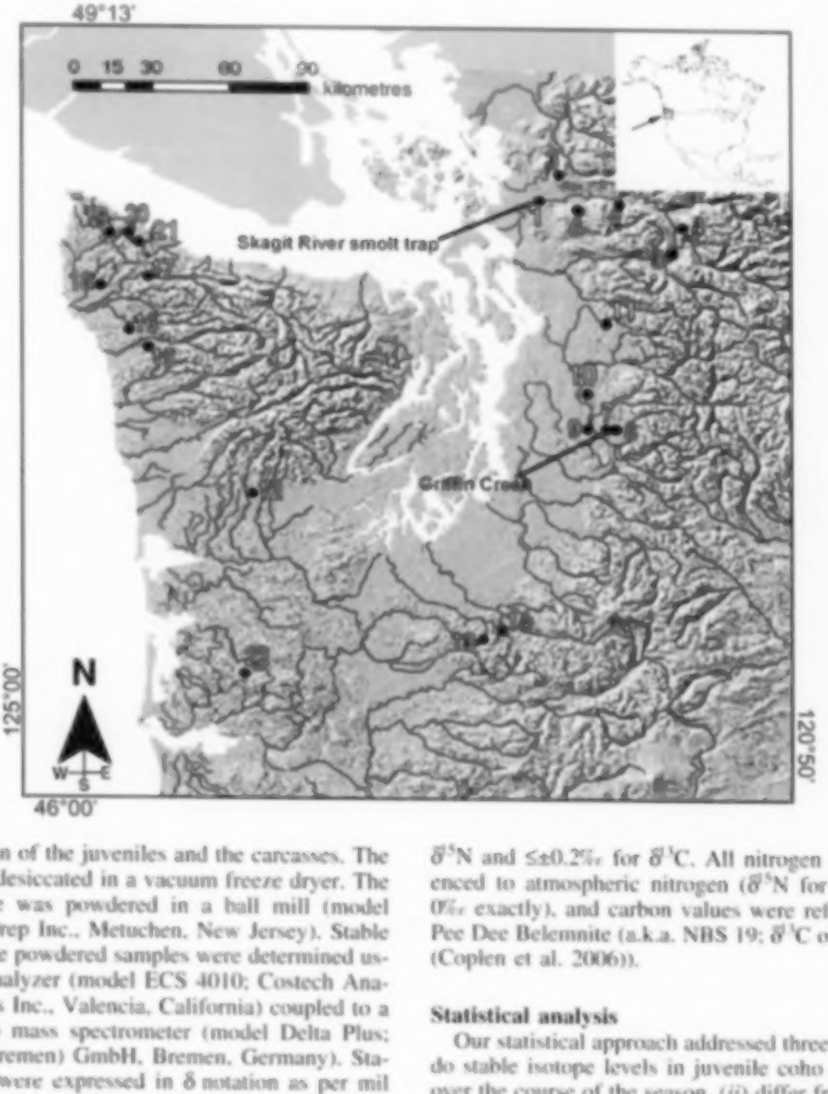
Effect of spawner density on δ^{15}N and δ^{13}C levels in juvenile coho salmon parr

We took dorsal muscle samples for stable isotope analysis from adult coho salmon carcasses in December of 1997, 2001, and 2002 from several reaches of Griffin Creek (Fig. 1), a third-order stream that is a tributary to the Snoqualmie River, Washington. Griffin Creek discharge for November through February is highly variable during this peak precipitation period and ranged from 0.3 to 1.1 m^3·s^{-1}, with high discharge events approaching 12.1 m^3·s^{-1} and extreme low discharge approaching 0.1 m^3·s^{-1} (King County Hydrologic Data for 2001, 2002, King County, Washington). An estimate of the total number of spawners within a reach was obtained from WDF&W spawner surveys using the area-under-the-curve method and assuming a life span at the survey reach of 10 days (Ames 1984). WDF&W stream survey data show the principal spawning period for coho salmon in Griffin Creek to be from early November through January. Presmolt coho salmon were collected from the spawning reaches by electroshocking in March 1992, 1993, 1996, 1997, 1999, 2001, and 2002. There were no adult coho salmon weight data available for the Snoqualmie River – Griffin Creek system. However, weight data were available for returning adult coho salmon in the Green River fishery just to the south of the Snoqualmie River and the average weight was 2.2 ± 0.3 kg (L. Weitcamp, Northwest Fisheries Science Center, NOAA-NMFS, Newport Research Station, 2032 SE OSU Drive, Newport, OR 97365-5275, USA). In addition, resident, native Griffin Creek cutthroat trout were collected in March by electroshocking above impassable barriers to provide background δ^{15}N and δ^{13}C tissue values.

Stable isotope ratio analysis

All fish and tissue samples were stored at –20 °C until processing. A section of muscle (10–30 mg) was taken adja-

Fig. 1. Map of western Washington showing where juvenile coho salmon (*Oncorhynchus kisutch*) were collected for stable isotope analysis. Sites (watershed): 1, Skagit River smolt trap at Mt. Vernon (Skagit), Wash.; 2, Finney Creek (Skagit); 3, Ennis Creek (Samish); 4, Hilt Creek (Skagit); 5, Mouse Creek (Skagit); 6, Parker Creek (Skagit); 7, Griffin Creek (Snoqualmie); 8, Grizzly Creek (Snoqualmie); 9, Patterson Creek (Snoqualmie); 10, Powerline Creek (Snoqualmie); 11, Worthy Creek (Snohomish); 12, Big Creek (Chehalis); 13, Huckleberry Creek (Deschutes); 14, Johnson Creek (Deschutes); 15, Winfield Creek (Hoh); 16, Hemp Hill Creek (Bogachiel); 17, Redoubt Creek (Soleduck); 18, Colby Creek (Dickey); 19, Cub Creek (Hoko); 20, Bear Creek (Hoko); 21, Charley Creek (Clallam); 22, Wasberg Creek (Willapa).



cent to the dorsal fin of the juveniles and the carcasses. The samples were then desiccated in a vacuum freeze dryer. The freeze-dried muscle was powdered in a ball mill (model 5100; SPEX CertiPrep Inc., Metuchen, New Jersey). Stable isotope ratios for the powdered samples were determined using an elemental analyzer (model ECS 4010; Costech Analytical Technologies Inc., Valencia, California) coupled to a stable isotope ratio mass spectrometer (model Delta Plus; ThermoElectron (Bremen) GmbH, Bremen, Germany). Stable isotope values were expressed in δ notation as per mil (‰) as defined by the following expression:

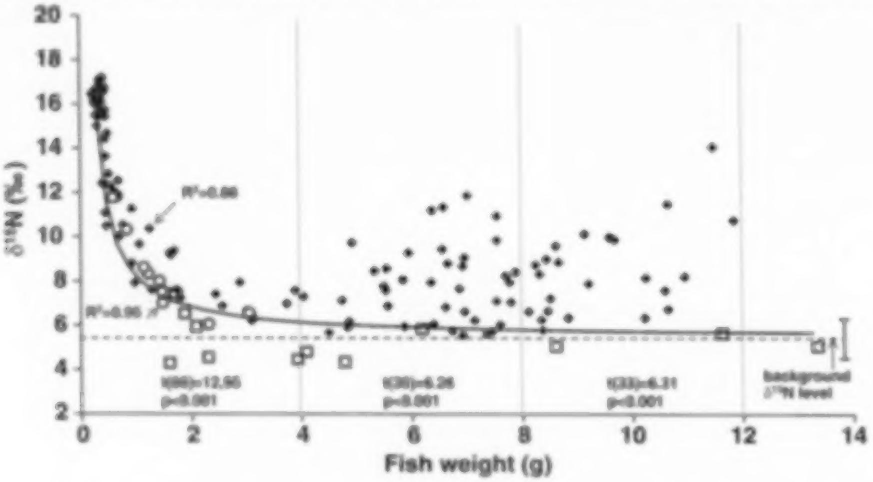
$$\delta Z = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where Z represents ^{15}N or ^{13}C, R_{sample} is the ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$ for samples, and R_{standard} is the ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$ for the corresponding standards. We used two standards each for N and C to define the line used to convert the mass spectrometer signal to sample $\delta^{15}N$ and $\delta^{13}C$ values, respectively. Precision for isotope analysis was ≤±0.3‰ for $\delta^{15}N$ and ≤±0.2‰ for $\delta^{13}C$. All nitrogen values were referenced to atmospheric nitrogen ($\delta^{15}N$ for atmospheric N is 0‰ exactly), and carbon values were referenced to Vienna Pee Dee Belemnite (a.k.a. NBS 19; $\delta^{13}C$ of NBS 19 = 1.95‰ (Coplen et al. 2006)).

Statistical analysis

Our statistical approach addressed three general questions: do stable isotope levels in juvenile coho salmon (*i*) change over the course of the season, (*ii*) differ from levels found in cutthroat trout above anadromous barriers, and (*iii*) increase as a function of spawner abundance? To address the first question, we assessed whether eq. 1 was a good approximation of $\delta^{15}N$ values by using regression to compare observed $\delta^{15}N$ values with those predicted by eq. 1, and by examining R^2 values of all Skagit River fish grouped by weight and those from Finney Creek only. In addition, we used quantile regression analysis (Scharf et al. 1998; Cade and Noon 2003) for analyzing $\delta^{15}N$ trends in Skagit coho salmon parr from February to early July 2005. This method is ideal for

Fig. 2. Coho salmon (*Oncorhynchus kisutch*) δ^{15}N data were plotted using fish weight as a surrogate for time (April 2004 to July 2005). The solid line (eq. 1) is a growth-dependent plot in which all additional growth above the initial weight is from system nutrients that would give a tissue value ~5.4 ± 1.0‰ (average ± standard deviation) for δ^{15}N (the value for cutthroat trout (*Oncorhynchus clarkii*) collected above impassible barriers). Solid diamonds represent coho salmon from Skagit smolt trap; open circles represent coho from Finney Creek, a Skagit tributary; and open squares are reference Skagit tributary cutthroat trout. Vertical lines denote size divisions of coho salmon. Results of *t* tests comparing each size group with cutthroat trout data are reported below the broken line. Actual degrees of freedom (df), or estimated df when variances were unequal, are in parentheses. R^2 values refer to proportion of variation explained by eq.1 regressed with Finney creek data or all other Skagit River data when coho salmon weighed less than 4 g.



assessing trends in a population containing subpopulations with different starting points. To address the second question, we separated fish into three groups based on weight or date of capture and used *t* tests to examine whether δ^{15}N and δ^{13}C levels in coho differed from those of a sample of 12 cutthroat trout captured above barriers. The cutthroat were captured over a three-week period, but differed in weight. However, stable isotope values did not change as a function of weight (for δ^{15}N, $R^2 = 0.02$, $F_{[1,10]} = 0.196$, $p > 0.05$; for δ^{13}C, $R^2 = 0.27$, $F_{[1,10]} = 3.86$, $p > 0.05$), so all cutthroat were included in each *t* test comparison. Where assumptions of equal variances were not met by Levine's test of homogeneity, we used *t* tests that assumed unequal variances. The third question was examined using linear regression analysis (Zar 1984) to compare spawner density data with δ^{15}N and δ^{13}C levels in coho salmon parr muscle. All data are presented as average ± standard deviation (SD). Level of significance was set at $p \leq 0.05$.

Results

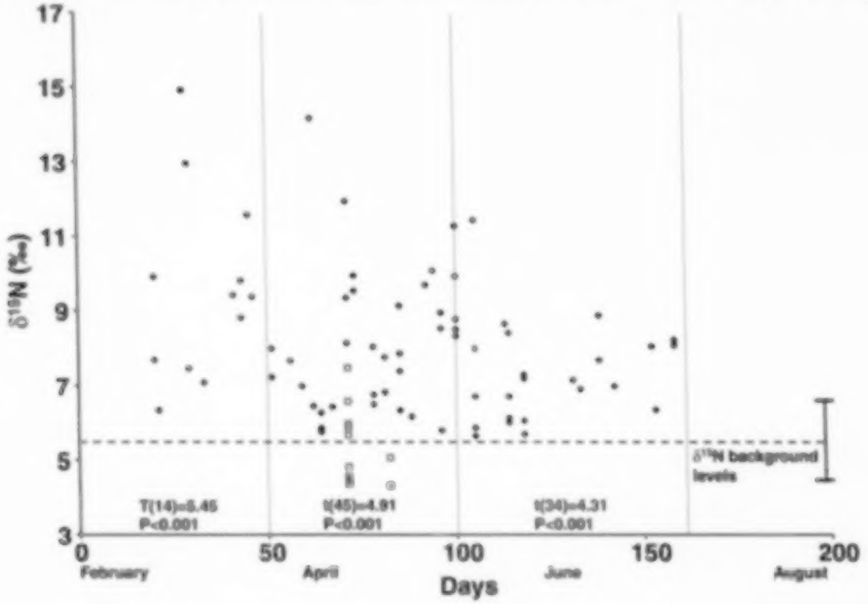
Seasonal variation of δ^{15}N and δ^{13}C in juvenile coho

Coho salmon fry exhibited the highest δ^{15}N values immediately after emergence during their freshwater residence period (muscle δ^{15}N ranged from 14‰ to 17‰). Because coho salmon emergence from gravel was spread over time, δ^{15}N data were plotted on the basis of weight versus δ^{15}N using weight as a nominal surrogate for time elapsed since emergence (Fig. 2). A growth-dependent model (eq. 1) was used to estimate the change in muscle δ^{15}N values with growth assuming that juvenile coho salmon after emergence were not exposed to MDNs and only consumed prey with δ^{15}N values similar to those available to cutthroat trout above an anadromous fish barrier. The mean δ^{15}N for cutthroat trout collected in early April was 5.4‰ ± 1.0‰ ($n = 12$) and was similar for cutthroat trout aged 0+ (5.4‰ ± 0.1‰, $n = 9$) and 1+ (5.3‰ ± 0.4‰, $n = 3$).

Our simple growth-dependent model was very good at predicting δ^{15}N values for fish collected within the Skagit River ($R^2 = 0.86$), especially for fish collected from one drainage within the Skagit River (Finney Creek, $R^2 = 0.95$), as long as fish weighed less than 2 g (Fig. 2). However, for larger fish, eq. 1 was not a good predictor of δ^{15}N values ($R^2 = 0.02$ and 0.23 for the second and third weight groups, respectively). Coho salmon δ^{15}N ratios declined exponentially until the fish were in the ~1.5 to 3 g range, which corresponded approximately to their size in October 2004. Most of the measured δ^{15}N values during this period were on or above the model line, indicating that their diet had the same or higher δ^{15}N as the reference cutthroat trout diet. The *t* tests confirmed that coho salmon δ^{15}N values of three size groups were significantly different from these cutthroat trout values (Fig. 2).

By the following March (2005), δ^{15}N was elevated in most overwintering coho salmon relative to fish sampled the previous summer (Fig. 3), but the isotope ratios exhibited considerable variability. Skagit coho salmon parr showed a decline in δ^{15}N from late February 2005 through July 2005 (Fig. 3), forming a wedge-shaped relationship between δ^{15}N and date of capture. Quantile regression analysis of the late February 2005 through July 2005 δ^{15}N data showed that the slope coefficient was negative for all quantiles but not significant for the low quantiles (0 to 0.6). The slope coefficient became significant ($p \leq 0.05$) for higher quantiles (0.6 to 1).

Fig. 3. Levels of δ^{15}N in Skagit coho salmon (*Oncorhynchus kisutch*) parr muscle from late February to early July 2005 (0 day = 1 February). Reference cutthroat trout (*Oncorhynchus clarkii*) δ^{15}N background level is 5.4‰ ± 1.0‰ (average ± standard deviation). Solid diamonds represent coho salmon and open squares are reference Skagit tributary cutthroat trout. Vertical lines denote temporal divisions of the data based on capture date. Results of *t* tests comparing coho in each temporal division with cutthroat trout data are reported below the broken line. Actual degrees of freedom (df), or estimated df when variances were unequal, are in parentheses.



which represent the quantiles of coho salmon parr that started with higher δ^{15}N values in February–March 2005. The quantile regression analysis shows that coho salmon parr δ^{15}N trends back towards the δ^{15}N values for reference cutthroat trout after exposure to carcasses during the winter months. Coho salmon δ^{15}N values from all three time periods were significantly different from values of cutthroat trout captured above barriers (Fig. 3).

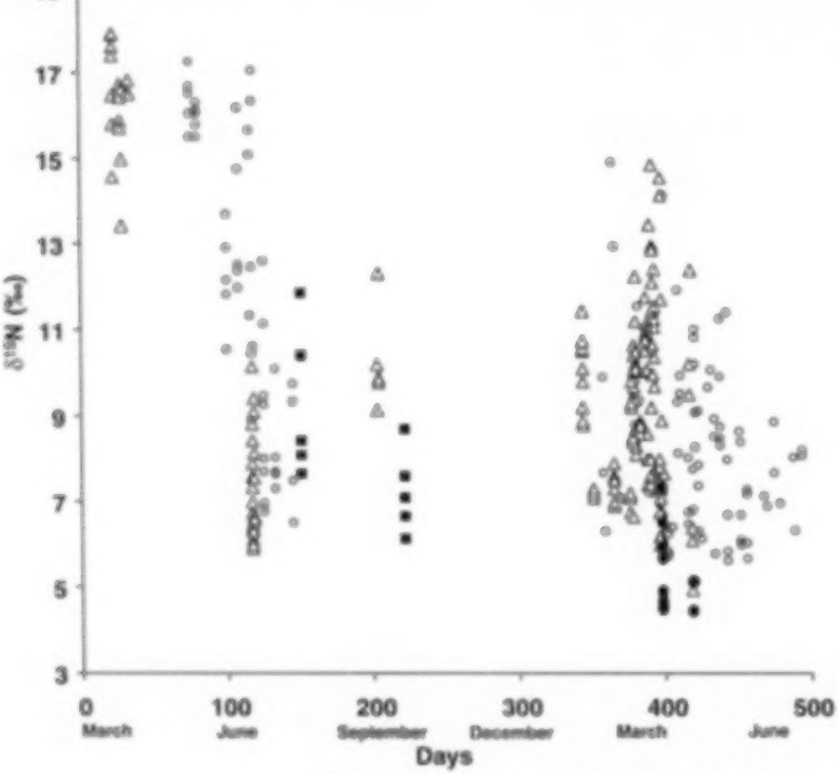
Additional stable isotope data for coho salmon juveniles have been collected at different times over several years from other western Washington streams in which coho salmon were the principal spawning species. A composite δ^{15}N profile of Skagit smolt trap δ^{15}N data and results for coho salmon juveniles from other western Washington streams overlap is shown (Fig. 4). These results suggest that this is a typical seasonal profile for western Washington coho salmon δ^{15}N levels. δ^{15}N values decline from emergence until the fall and then increase until March followed by a declining δ^{15}N signal until the early summer.

Coho salmon δ^{13}C showed a different pattern than δ^{15}N. Like δ^{15}N data, the δ^{13}C values (−16‰ to −17‰) in post-emergence coho salmon fry were the highest measured compared with any other time during the freshwater sampling period (Fig. 5). Fish weighing 4 g or less had significantly higher δ^{13}C values than cutthroat trout living above barriers. However, at larger sizes (fish weight 4–12 g), δ^{13}C values for juvenile coho salmon were not significantly different from the background values for reference cutthroat trout and continued to remain that way until the end of the study (Fig. 5). Hence, unlike the δ^{15}N data, we did not observe an increase in δ^{13}C levels in larger fish with access to coho carcasses. There was also much more variability in δ^{13}C values. δ^{13}C values for coho salmon parr varied as much as 12‰ (−34‰ to −22‰) from fall 2004 on. Reference age-0+ and age-1+ cutthroat trout showed little difference in δ^{13}C levels. Cutthroat δ^{13}C values (n = 12) were −25.7‰ ± 1.8‰ (−29‰ to −24‰) and had less range than those for coho salmon.

Effect of spawner density on δ^{15}N and δ^{13}C levels in juvenile coho salmon parr

In Griffin Creek, we found a strong relationship (p < 0.001, R^2 = 0.45) between δ^{15}N values in the coho salmon parr collected in March and coho salmon carcass density (kg·km^{-1}) based on WDF&W stream surveys (Fig. 6a). At higher spawner densities (≥1300 kg·km^{-1}), some parr approached carcass δ^{15}N levels (14.1‰ ± 0.5‰). At 1800 kg·km^{-1}, some parr δ^{15}N values exceeded those of adult coho salmon carcasses. A significant relationship (p < 0.01, R^2 = 0.20) between δ^{13}C levels in Griffin Creek coho salmon parr and spawner density was also found (Fig. 6b). However, unlike δ^{15}N for parr, the juvenile δ^{13}C levels approached but did not attain average adult carcass values (−16.6‰ ± 0.4‰, range −17.5‰ to −15.8‰) at higher spawner densities. The highest δ^{13}C value measured for parr was still ~4‰ lower than carcass levels. Composite reference cutthroat trout stable isotope values (n = 6) for two different years (1996 and 1997) from East Fork Griffin Creek for δ^{15}N is 7.7‰ ± 0.3‰ (range 7.4‰ to 8.1‰) and for δ^{13}C is −28.1‰ ± 0.9‰ (range −29.3‰ to −26.9‰). In 1996 (n = 3), δ^{15}N is 7.7‰ ± 0.3‰ and δ^{13}C is −28.9‰ ±

Fig. 4. δ^{15}N levels present in juvenile coho salmon (*Oncorhynchus kisutch*) (ages 0+ and 1+) from western Washington streams (open triangles) that were collected from multiple sites in different years (nominal age day 0 = 1 March). Skagit coho salmon study data are represented by open circles, coho salmon from Finney Creek by solid squares, and reference cutthroat (*Oncorhynchus clarkii*) by solid circles.



0.5‰. In 1997 ($n = 3$), δ^{15}N is 7.7‰ ± 0.3‰ and δ^{13}C is −27.4‰ ± 0.4‰.

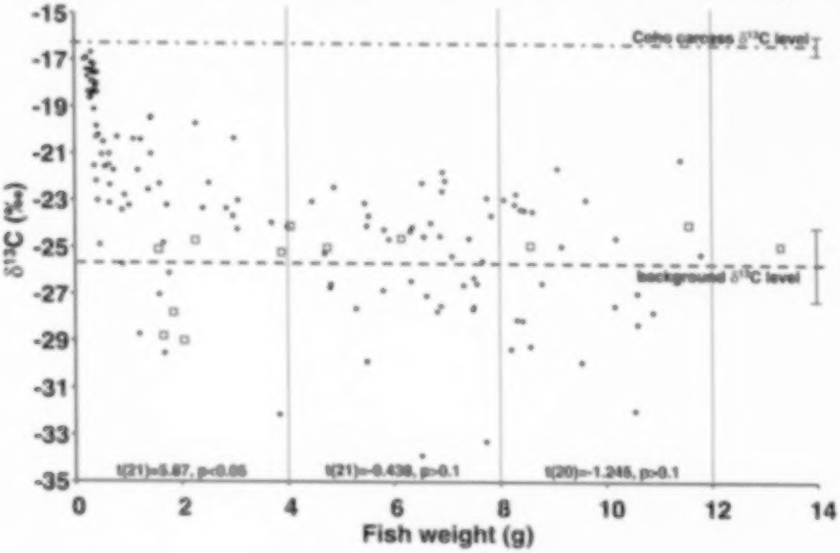
Discussion

The composite δ^{15}N tissue values in coho salmon juveniles represent the integration of their starting δ^{15}N levels and δ^{15}N from carcasses and other dietary sources. Initially, we observed a strong negative trend in young-of-the-year coho salmon δ^{15}N levels, indicating that their diet is not strongly influenced by nitrogen from MDN sources up to early fall. The period from November through January represents the principal time in western Washington streams when juvenile coho salmon have access to adult coho salmon carcass material or eggs for direct consumption (Michael 1998). In March 2005, after a winter of feeding on available carcasses and eggs, coho salmon parr have a wide range in both weight (2–11 g) and δ^{15}N values (~6.3‰ to ~14‰) that are indicative of variable carcass availability. The finding that the δ^{15}N signal in coho salmon juveniles in the early fall was approaching the reference δ^{15}N levels of cutthroat trout and the low variability of δ^{15}N in salmon carcasses strongly suggest that the fraction of δ^{15}N from MDNs in coho salmon parr tissue after the spawning season could be estimated using a simple mixing model:

$$P = (S + 3)F + C(1 - F) \tag{2}$$

where P represents δ^{15}N for coho salmon parr in March and is a composite value for tissue from MDNs and watershed derived nutrients; the term $(S + 3)$ includes spawner δ^{15}N and the trophic enrichment component of ~3‰ (Minigawa and Wada 1984) that occurs when the juveniles consume carcass material; F is the fraction of MDN-derived tissue from salmon carcasses; the term $(1 - F)$ is the tissue fraction from the baseline reference diet contributing to growth during the winter and coho tissue present at the start of spawning season; and C is the reference δ^{15}N for cutthroat trout muscle and represents tissue δ^{15}N formed from watershed-derived nutrients and not MDNs. A simple estimate of the MDNs fractional contribution to growth can be made by solving for F. For example, if δ^{15}N for a March coho salmon parr is 12.3‰, carcass δ^{15}N is 14‰, and the cutthroat trout reference δ^{15}N is 5.4‰, then the estimated fraction of MDN-derived tissue would be 0.59. The ability to estimate F and the information in Fig. 6 suggest that if graphs of carcass density versus tissue δ^{15}N levels are available, then assessment of adult escapement to a tributary from δ^{15}N levels present in March juvenile coho parr is possible. However, this requires that the carcass density data versus juvenile coho δ^{15}N levels have been generated for a stream of similar characteristics and that an adequate group of coho parr was

Fig. 5. δ^{13}C levels present in juvenile Skagit River coho salmon (*Oncorhynchus kisutch*) were plotted using fish weight as a surrogate for time (April 2004 to July 2005). Fish in the fall weighed from 2.5 to ~3 g. Reference cutthroat trout (*Oncorhynchus clarkii*) δ^{13}C is −25.7‰ ± 1.8‰ (average ± standard deviation). Solid diamonds represent coho salmon and open squares are reference Skagit tributary cutthroat trout. Vertical lines denote size divisions of coho salmon. Results of *t* tests comparing each size group with cutthroat trout data are reported above the *x* axis. Actual degrees of freedom (df), or estimated df when variances were unequal, are in parentheses.

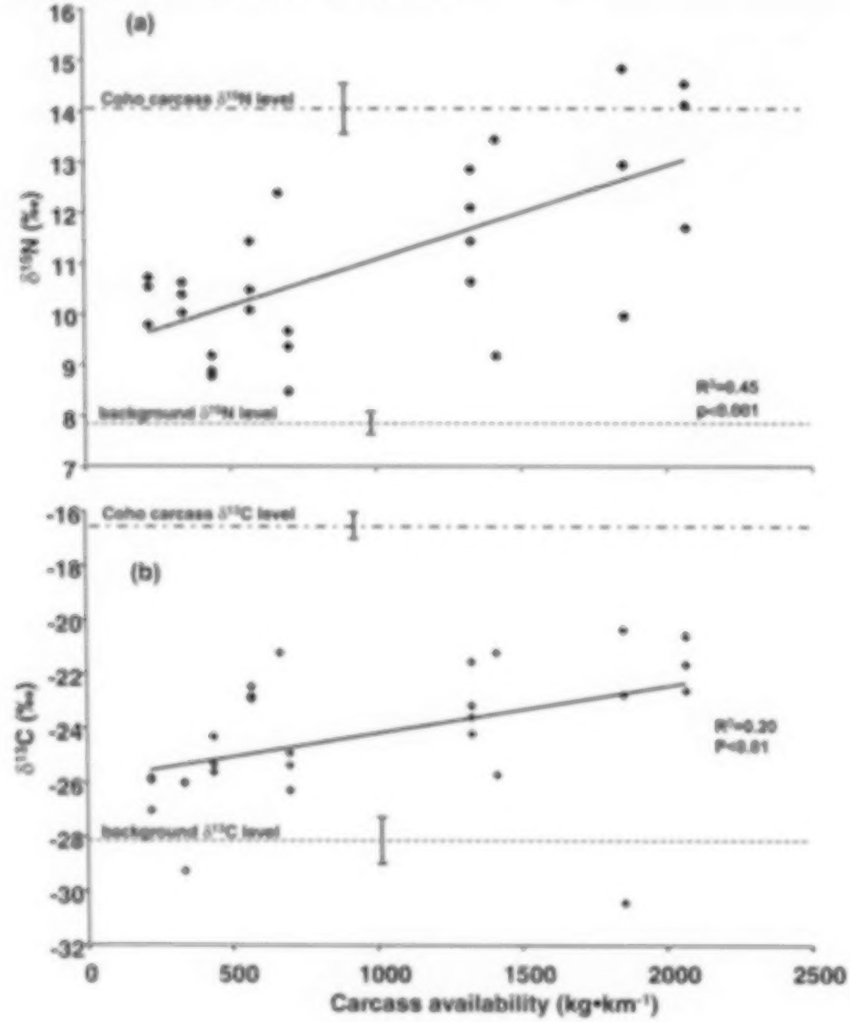


sampled immediately after the spawning season. Our data from other watersheds (data not shown) indicate that δ^{15}N values in reference cutthroat trout can vary and would need to be determined for each watershed. In addition, δ^{15}N for salmon carcasses can vary by several parts per thousand (‰) between species, and if juvenile salmonids were feeding on carcasses from several species of salmon, this could introduce a small error in the estimate of MDNs accumulated in tissues. Also, the presence of agricultural and sewage inputs in juvenile rearing habitats may be a confounding factor. However, this approach should be useful in evaluating the extent to which carcasses are being utilized by juvenile coho salmon and, by extension, whether spawning salmonid escapement goals allow for sufficient MDN additions by returning adults.

Juvenile coho salmon would also have been feeding on available invertebrates during this overwintering period. Bilby et al. (1996) showed that invertebrate δ^{15}N values increase in the presence of carcasses and ranged from 4‰ to 9‰. However, invertebrate δ^{15}N values do not approach carcass δ^{15}N levels. Even if one accounted for the ~3‰ trophic enrichment factor when consuming aquatic invertebrates, fish could not reach the levels observed in some juvenile coho salmon that had access to carcasses with a δ^{15}N value of ~14‰. Moreover, the winter season is a period of low invertebrate productivity. Only carcasses (~14‰) and eggs (~16‰) from spawning salmon would have high enough δ^{15}N values to raise coho salmon juvenile tissue δ^{15}N from early fall levels to some of the levels observed in this study. The variability of δ^{15}N data in March and April indicates that an appreciable proportion of the overwintering juveniles either had limited access to carcass material or that a sufficient amount of food with low δ^{15}N values was ingested to offset any isotopic response to carcass materials. These δ^{15}N data suggest that there were subpopulations (quantiles) of coho salmon parr exposed to different levels of carcasses. We used the quantile regression analysis approach to parse out seasonal patterns by subpopulations. The significant decline in the signal in coho salmon parr tissues in the higher δ^{15}N quantiles (0.6 to 1) after March implies that once carcasses are no longer available, the fish consume items with much lower δ^{15}N values. In addition, the general overlap of δ^{15}N values from other western Washington streams and the Skagit suggests that this is the typical seasonal pattern for the δ^{15}N signal in coho salmon juveniles. The seasonal trends in the δ^{15}N signal supports the contention by Bilby et al. (1996) that the signal increases in tissues when carcasses are available and then declines during the rest of the year.

The presence of dairy farms in the mid- to lower Skagit and large towns in the lower Skagit raise the possibility that waste and (or) manure effluents may influence δ^{15}N levels. The four streams where reference cutthroat trout were collected are upstream of these areas and not adjacent to or downstream of dairy-farming areas. The fact that the δ^{15}N signal in juvenile age-0 coho salmon was approaching the values determined for reference cutthroat trout would indicate that manure and (or) sewage waste was not materially affecting δ^{15}N signal in the juvenile coho salmon food chain. In addition, the coho salmon δ^{15}N values went up during the winter months during the presence of carcasses; this is also a period when flows are higher because of increased precipitation, which would dilute the isotopic signal from sewage–manure inputs. Also, a review of the literature for west coast salmon spawning streams did not reveal any significant references to other sources of high value δ^{15}N aside from MDNs that would cause the level of increase in the δ^{15}N val-

Fig. 6. March levels of (*a*) δ^{15}N and (*b*) δ^{13}C present in coho salmon (*Oncorhynchus kisutch*) parr from Griffin Creek, a tributary to the Snoqualmie River in western Washington, at different spawner densities. Coho salmon carcass δ^{15}N levels were 14.1‰ ± 0.5‰ ($n = 20$, average ± standard deviation (SD)), and δ^{13}C levels were −16.6‰ ± 0.4‰ ($n = 20$, average ± SD). Reference cutthroat trout (*Oncorhynchus clarkii*) δ^{15}N is 7.7‰ ± 0.3‰ and δ^{13}C is −28.1‰ ± 0.9‰.



ues observed in some of the coho age-1+ juveniles. Our findings show the stable isotope profiles in juvenile coho salmon are consistent with seasonal exposure to carcasses.

Our analysis of the δ^{15}N signal in cutthroat trout suggests that it does not vary significantly over the course of a year. Although we do not have a full year of δ^{15}N data for cutthroat trout, we have data for several years from the same site and also for two age groups of reference cutthroat trout collected in early April after the coho salmon spawning period. The δ^{15}N values are similar from year to year at the same site, and there are minimal differences between age-0+ and age-1+ cutthroat trout. The coho salmon juveniles below the anadromous barriers are exposed to a similar diet except when carcasses are present. In the absence of carcasses, coho salmon δ^{15}N levels trend towards cutthroat trout values. The first-year coho salmon δ^{15}N values follow closely to the model line in Fig. 2, which is based on the assumption that they are consuming an isotopically similar diet to that of the cutthroat trout. These findings support the contention that the isotopic value of cutthroat trout muscle does not change significantly after dilution of the maternal contribution by growth and represents watershed inputs.

In contrast to the δ^{15}N trends in Skagit River juvenile coho salmon, δ^{13}C values did not appear to be strongly influenced by the presence of spawning salmon. After an initial drop in δ^{13}C following emergence from the gravel, δ^{13}C values in coho salmon averaged close to that seen in reference cutthroat trout collected above anadromous barriers but had a wider range. The high δ^{13}C variability suggests that the juvenile coho salmon were consuming items with a very wide range of δ^{13}C values. Hicks et al. (2005) found that aquatic invertebrates from coho salmon rearing habitats in the Copper River Delta, Alaska, had a broad range in δ^{13}C values (approximately –25‰ to –40‰). Invertebrates from pool habitats have higher δ^{13}C values than those from riffle habitats (Findlay et al. 2002). Terrestrial vegetation typically exhibits a δ^{13}C value much lower than that of algae growing in the stream (Bilby et al. 1996). As a result, fish feeding on terrestrial invertebrates will exhibit lower δ^{13}C values than fish at sites where aquatic invertebrates are the predominant food source. These factors would help to explain the variability in δ^{13}C values in older juvenile coho salmon. If direct consumption of eggs and carcass tissue were occurring, a response would be expected in both the N and C values by the following March. In fact, there was a positive relationship between the amount of carcass tissues deposited and δ^{13}C values for coho salmon parr from Griffin Creek, a stream that supports high densities of spawning coho salmon. The lack of response in the Skagit River fish may be that carcass deposition was not great enough to generate a detectable change in the δ^{13}C value. The high variability of δ^{13}C in Skagit juvenile coho salmon throughout the summer also may contribute to the difficulty in detecting a δ^{13}C increase with the arrival of spawning salmon. In addition, metabolic fractionation causes a ~3‰ increase in δ^{15}N above the isotope ratio for ingested material (Minigawa and Wada 1984), which enhances the δ^{15}N change, whereas only a ~1‰ fractionation effect occurs for δ^{13}C. In summary, the results from Griffin Creek, a small tributary to the Snoqualmie River, indicate a definite but not strong relationship between carcass availability and δ^{13}C values in coho parr. However, juvenile coho salmon from the Skagit represent a sample from a much larger drainage in which the variability of tributary δ^{13}C signatures based on habitat inputs or anthropogenic influences (Doucett et al. 1996) appear to be greater than that for Griffin Creek. At present, the factors affecting δ^{13}C values in juvenile coho salmon are not clearly understood and need further investigation.

The variability of both δ^{15}N and δ^{13}C in juvenile coho salmon from the Skagit River and the relationship between density of spawning salmon and the δ^{15}N and δ^{13}C levels suggest that carcass availability plays a key role in determining seasonal shifts in isotopic values. It has been previously suggested that the relationship between spawner abundance and the isotopic signature of juvenile fishes could be used to help identify escapement goals that would enhance the nutritional status of streams (Bilby et al. 2001). Our data support that contention. If sufficient carcass tissue is available, isotopic values in juvenile coho salmon can achieve levels approaching those in adult fish. We found δ^{15}N values in some Skagit River coho salmon parr in March approaching 15‰, and some juvenile fish from Griffin Creek exhibited comparable values during years of high escapement. A significant proportion of the diet would need to be composed of carcass flesh or eggs for the juvenile fish to exhibit a δ^{15}N value this high. A δ^{15}N level for coho salmon parr in March of 12‰ to 14‰ would be indicative of abundant ingestion of materials from spawning salmon, whereas levels of 7‰ or below may represent a situation in which salmon carcass and eggs are minimally available and may be impacting system productivity. Further study assessing the relationship between the density of spawning salmon, the δ^{15}N levels in juvenile salmonids, and the associated productivity of the fish population will help to determine whether stable isotope analysis can be developed into a useful tool to aid in the establishment of escapement goals.

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Optimal harvesting considering biological and economic objectives

Brian G. Bue, Ray Hilborn, and Michael R. Link

Abstract: Most examinations of optimal harvesting policies have considered only biological objectives, yet it is increasingly recognized that a primary objective of many fisheries is economic profitability. Using Bayesian risk analysis, we compare policies that combine fish harvesting, the revenue brought in by fish sales, the cost of harvesting and processing, and processing and fishing capacity to find policies that maximize biological yield and economic profit to the processing and harvesting sectors for a major Pacific salmon (*Oncorhynchus* spp.) fishery in Bristol Bay, Alaska. We show that although average catch is maximized by a fixed escapement policy, total revenue is maximized by a policy that includes some harvesting at stock sizes below that required to produce maximum average catch. In addition, there is a wide range of policies that provide 90% of the maximum for any of the biological and economic objectives considered. Economic profitability is enhanced by limitations on processing and harvesting capacity.

Résumé : La plupart des examens des politiques optimales de récolte ne tiennent compte que des objectifs biologiques, bien qu'il soit de plus en plus reconnu que l'un des buts principaux visés par de nombreuses pêches commerciales est la rentabilité économique. À l'aide d'une analyse bayésienne des risques, nous comparons des politiques qui combinent la récolte des poissons, les revenus générés par les ventes de poissons, les coûts de la récolte et de la transformation, ainsi que les capacités de pêche et de transformation, afin de trouver des politiques qui maximisent le rendement biologique et le profit économique aux secteurs de la pêche et de la transformation, dans le cas d'une importante pêche commerciale de saumons du Pacifique (*Oncorhynchus* spp.) dans la baie de Bristol, Alaska. Nous montrons qu'alors que la capture moyenne est maximisée par une politique d'échappement fixe, le revenu total est maximisé par une politique qui inclut certaines récoltes à des tailles de stocks qui sont inférieures à celles nécessaires pour produire des captures moyennes maximales. De plus, il existe une gamme étendue de politiques qui permettent d'atteindre 90 % du maximum de chacun des objectifs biologiques et économiques considérés. Des restrictions sur la capacité de pêche et de transformation augmentent la rentabilité économique.

[Traduit par la Rédaction]

Introduction

The theory of optimal harvesting suggests that maximization of biological yield is achieved by holding the spawning population at a constant level (Clark 1976). This population size is commonly referred to as the biomass that produces maximum sustainable yield (B_{MSY}), and the escapement goal and harvest policies that hold spawning stock constant are referred to as fixed escapement policies (Hilborn and Walters 1992). Among the few commercial fisheries that are theoretically managed for fixed escapement are most of Alaska's terminal Pacific salmon (*Oncorhynchus* spp.) fisheries. For these fisheries, the annual harvest is manipulated by in-season regulation in an attempt to hold the spawning stock size within a range close to the calculated B_{MSY} (Minard and Meacham 1987; Fair 2003).

Alaskan salmon fisheries have been biologically successful, with record catches occurring in many areas since the late 1970s (Eggers 1992). It is not clear how much of this success can be attributed to either the escapement policies or favorable environmental conditions (Hilborn 2006). However, the economic success of the fisheries in the 1980s and 1990s has evaporated as salmon prices have declined dramatically because of increasing competition with farmed salmon from Chile and wild salmon from Russia (Asche et al. 1999; Hilborn 2006; Knapp et al. 2007). Coincidental with the decline in the price of salmon, the value of fishing permits collapsed and fishermen are struggling to stay in business, with many unable to operate (Link et al. 2003; Schelle et al. 2004). The decline in value of fishing permits reflects the decline in expected future earnings in the fishery (Karpoff 1984, 1989; Huppert et al. 1996).

Although the average economic profit for drift gillnet vessels in Bristol Bay from 1982 to 1996 was between US$13 000 and US$47 000, the fishery now operates at a net loss (Schelle et al. 2004), with average profit negative for all

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years between 1997 and 2003 except 1999. Link et al. (2003) reported that in 2001, permit holders averaged US$4 000 in income after operating costs, but before debt service on permits and vessels. Given the large number of unused permits in other Alaskan salmon fisheries and the low market value of limited entry permits, the economic results in Bristol Bay are likely typical of most Alaskan salmon fisheries. Economic returns to fish processors have paralleled those of the fishermen.

The traditional assumption of Alaskan fisheries management has been that if the resource was managed to produce maximum sustained yield, the economics would take care of itself. In contrast, economists have long recognized that the economically optimal harvesting policy is not the same as the policy that maximizes sustainable biological yield (Gordon 1953; Scott 1955; Clark 1976). The Bristol Bay sockeye salmon (*Oncorhynchus nerka*) fishery contributes such a large volume of catch to the world market that it affects the worldwide price. Knapp (2004) has estimated (under specific assumptions about the price of farmed fish in Japan) that when the Bristol Bay catch is 10 million fish, the price would be US$1.43·kg^{-1} ex-vessel, and if the catch was 30 million fish, the price would be US$0.79·kg^{-1}. This has clear implications on the selection of a harvest policy. The basic logic of the fixed escapement policy is that if the expected production of one additional fish in the spawning stock produces one or more fish in the future, then that fish should be added to the spawning stock, whereas if the expected production of one additional fish in the spawning stock is less than one, then that fish should be harvested now. If the objective is to maximize the economic value of the catch, then the optimum number of fish in the escapement or catch will depend on the size of the return. When the salmon run is small and little catch is expected, the economic value of a fish in the catch is above average, and the expected number of fish produced by an additional spawner will need to be large enough to offset the differential in price between the present and future salmon returns. A priori, we would expect that maximization of revenue would suggest some harvesting at total salmon returns lower than the traditional optimum biological escapement.

The economic profitability of the harvesting sector depends on the size and efficiency of the fishing fleet. It has been estimated that the optimal number of drift net licenses for the Bristol Bay sockeye salmon fishery is about 800–1200 rather than the current 1858 (Schelle et al. 2004). A considerably smaller fishing fleet operating under the present vessel and gear restrictions would most likely be unable to harvest large catches. Charles (1983) has shown for marine fisheries that revenues are maximized by a combination of harvesting and investment strategies and that there is a maximum level of harvesting capacity. Similarly, there is presumably a maximum optimum processing capacity; the fixed costs in maintaining large processing plants that might only be fully utilized for a week every few years would far outweigh the profit from the additional fish processed.

We expect that maximization of revenue will suggest some harvesting at total salmon returns lower than the traditional optimum escapement and a maximum level of harvest constrained by the fixed costs of harvesting and processing. In this paper, we will present a methodology for evaluating a wide range of harvest policies taking into account biological and economic factors and illustrate the use of these methods for the sockeye salmon return to the Egegik River, Bristol Bay, Alaska.

Materials and methods

Model formulation

We examined a wide range of harvest policies to determine where both biological and economic objectives are optimized through a modeling process. The model was made up of three distinct components: (*i*) a salmon production submodel in which historic catch, escapement, and age data were combined to simulate the escapement to total salmon return relationship and evaluate the uncertainty in such relationships using Bayesian analysis; (*ii*) a harvest policy submodel in which a wide range of harvest policies was applied to each year's simulated salmon return to generate catches; and (*iii*) an economic submodel in which revenue and costs for both fishing and fish processing were combined with the simulated harvests to estimate net present value to the harvesting and processing sectors.

Salmon production submodel

A spawner–recruit relationship was used to drive the population dynamics of the modeled salmon returns. The relationship was estimated from historical catch and escapement data, which had been tabulated into brood tables (Hilborn and Walters 1992). Although several different models can be used, we present the formulation for the Beverton–Holt model:

$$(1)\qquad R_t = \frac{S_t}{\dfrac{1}{\alpha} + \dfrac{S_t}{\beta}}\exp(w_t)$$

where S_t and R_t are the spawning stock and subsequent salmon return for brood year t, respectively, and w_t is the process error in brood year t. Autocorrelation in the process error associated with the fit of the model to the historic data was accounted for by

$$(2)\qquad w_t = zw_{t-1} + \sigma_{w^*} \cdot w_t^* \sqrt{1-z^2}$$

where w_t^* is the white noise random error at brood year t with mean 0 and standard deviation 1, z is the autocorrelation term, and σ_{w^*} is the standard deviation of the random process error component (Morris and Doak 2002). The value for w_t^* can be found by

$$(3)\qquad w_t^* = \frac{w_t - zw_{t-1}}{\sigma_{w^*} \cdot \sqrt{1-z^2}}$$

The likelihood for the Beverton–Holt spawner–recruit model that incorporates autocorrelation in the process error can be written as

$$(4)\qquad L[R|\alpha, \beta, \sigma_{w^*}, z] = \prod_t \frac{1}{\sigma_{w^*} \cdot \sqrt{2\pi}} \exp\left(\frac{-(w_t^*)^2}{2\sigma_{w^*}^2}\right)$$

The above equations are sufficient to find the maximum likelihood estimates of the parameters. However, when evaluating the consequences of any harvest policy for Pacific salmon, particularly the interannual variability in catch or spawning stock, it is important to incorporate age at salmon return information rather than simply considering brood-year salmon returns. For this application, age structure was modeled using the Dirichlet distribution and the methods developed by Evans et al. (2000). The Dirichlet distribution is the multivariate form of the beta distribution, which is sometimes used to model the Bernoulli parameter defining the probability in a success–failure situation. This distribution generalizes the beta in that it can be used to model more than one "yes" or "no" parameter at once. Random numbers generated from both the beta and Dirichlet distributions lie between zero and unity, making them suitable for generation of proportions.

The form of the Dirichlet distribution is

$$(5)\qquad f(\theta\,|\,\alpha_1,\ldots,\alpha_K) = \frac{\Gamma(\alpha_1+\ldots+\alpha_K)\,\theta_1^{\alpha_1-1}\ldots\theta_K^{\alpha_K-1}}{\Gamma(\alpha_1)\ldots\Gamma(\alpha_K)}$$

where α_k are parameters of the Dirichlet distribution and θ_k is the proportion of age class k subject to the constraints θ_1, …, $\theta_k \geq 0$ and $\Sigma_{k=1}^{K}\theta_k = 1$. A Dirichlet distribution was fitted to m years of historical age-class data using maximum likelihood. The log likelihood for m years of observations is

$$(6)\qquad \ln[L(\alpha\,|\,\theta_m)] = \sum_{m=1}^{M}\left[\ln\Gamma(\alpha_0) - \sum_{k=1}^{K}\ln\Gamma(\alpha_k) + \sum_{k=1}^{K}(\alpha_k - 1)\ln(\theta_{km})\right]$$

with

$$\alpha_0 = \sum_{k=1}^{K}\alpha_k$$

A multivariate random vector was sampled from the fitted Dirichlet distribution for each brood year with the resulting vector defining the nature of the age class for that simulated brood-year return.

Harvest strategy submodel

A wide range of harvest policies including constant escapement, constant harvest rate, and constant catch can be simulated using a simple linear model in which catch is a linear function of total salmon return. Catch for this model is constrained to be less than the total salmon return and greater than or equal to zero (Hilborn and Walters 1992). For example, a constant harvest rate policy can be simulated by a linear function with intercept zero and slope equal to the harvest rate, a constant escapement policy can be simulated using a linear function with a slope of 1.0 and an intercept of negative the escapement goal, and a constant catch policy has a slope of zero and an intercept equal to the constant catch. We can further modify this submodel by capping the catch at a maximum. We call this type of policy a "floor–ceiling model" in which "floor" is the size of the salmon return at which harvesting begins, "harvest rate" is the slope of the line, and "ceiling" is the maximum harvest. Note that the "harvest rate" in this terminology is only the fraction of all salmon returns harvested if the "floor" is zero. It could more properly be called the "marginal harvest rate", i.e., the fraction of the salmon return that would be harvested. This harvest strategy model has the potential of identifying the combination of escapement goal, harvest rate, and catch ceiling that has the greatest potential of maximizing parameters such as yield or net present value. The model can be written as

$$(7)\qquad \hat{C}_y = \begin{cases} C_{\max} & \text{if } -E + \mu\hat{T}_y > C_{\max} \\ -E + u\hat{T}_y & \text{if } \hat{T}_y > E \\ 0 & \text{if } \hat{T}_y < E \end{cases}$$

where $\hat{T}_y$ is the estimated total salmon return in year y, $\hat{C}_y$ is the estimated catch for year y, $C_{\max}$ is the ceiling or maximum allowable catch, E is the escapement floor, and u is the marginal harvest rate subject to the constraint $0 \leq u \leq 1.0$. We can use this generalized harvest strategy to identify the combination of E, u, and $C_{\max}$ that maximizes a desired outcome (e.g., catch and economic profits).

Economic submodel

An economic submodel was developed to characterize how the economic value of the catch from a single fishery changes across harvest policies. Income to the processors and fishermen was modeled using the August Japanese wholesale and ex-vessel price for Bristol Bay sockeye salmon, whereas the cost of processing the catch and harvesting the fish was estimated using previously developed models for the Bristol Bay sockeye salmon fishery (Link et al. 2003). Combining the production, harvest, and economic models into a single simulation allows for the estimation of the long-term value of the catch or net present value (NPV) for a wide range of harvest policies.

August Japanese wholesale price for Bristol Bay sockeye salmon and the magnitude of the catch were used to estimate revenue to the fish processors. Knapp (2004) estimated ex-vessel price for Bristol Bay sockeye salmon using the volume of the Bristol Bay sockeye salmon harvest and the wholesale price of farmed Coho salmon (*Oncorhynchus kisutch*) in Japan. In addition, Knapp (2004) and Holzinger (2007) implied that the Japanese wholesale price for Bristol Bay sockeye salmon was directly related to the ex-vessel price. We assumed that the August wholesale and ex-vessel prices were linearly related and developed a relationship based on the findings of Knapp (2004) to calculate the August Japanese wholesale price for Bristol Bay sockeye salmon in 2003 dollars per kilogram that would be paid in year y of our simulation using

$$(8)\qquad P_{\text{whole},y} = \exp[4.82 + (-0.35\ln B_y) + (0.96\ln P_{\text{coho},y}) + \varepsilon_{\text{whole},y}]$$

where $P_{\text{whole},y}$ is the August Japanese wholesale price of Bristol Bay sockeye salmon, B_y is the biomass of the Bristol Bay sockeye salmon harvest in metric tons, $P_{\text{coho},y}$ is the wholesale price of farmed coho salmon in Japan, and $\varepsilon_{\text{whole},y}$ is the process error. The data came from Knapp (2004) for the years 1991–2003 and from G. Knapp (personal communication, 2007) for the years 2004–2006. Because we had no means of estimating $P_{\text{coho},y}$ for our simulations without de-

Table 1. Parameters used to simulate operating costs for shore-based and floating salmon processors in Bristol Bay, Alaska (Link et al. 2003).

	Processor type	
	Shore-based	Floating
Operating parameters		
Processor capacity (in no. of fish)	1 600 000	800 000
Product recovery rate	0.77	0.80
Fixed costs (facility overhead)	$1 900 000	$1 500 000
Variable costs for raw fish		
Cost for fish (ex-vessel price)[a]	$P_{\text{ex},y}$	$P_{\text{ex},y}$
Tendering cost	$0.37	$0.29
Fish tax	$0.04	$0.07
Variable costs for processing fish		
Cost purchased for labor	$0.44	$0.46
Cost purchased for packaging	$0.22	$0.11
Cost purchased for miscellaneous	$0.02	$0.02
Cost purchased for utilities (fuel, water, etc.)	$0.09	$0.18
Carrying cost	$0.02	
Freight cost	$0.09	
Total variable cost purchased[b]	$\$1.29 + P_{\text{ex},y}$	$\$1.13 + P_{\text{ex},y}$

Note: Costs (including taxes) are per kilogram in US dollars.

[a] From eq. 9.

[b] Total variable cost is the sum of the raw fish and processing variable costs.

veloping another model for worldwide farmed coho production, we assumed that $P_{\text{coho},y}$ would be the average price paid for the years 2000–2006 (US$4.25·kg^{-1} in 2003 dollars) for all years in the simulation. It was also assumed that the average weight of sockeye salmon was 2.68 kg for the conversion of numbers of fish obtained from the harvest policy model into biomass. Process error was simulated by drawing a random normal deviate with a mean of zero and a standard deviation of 0.124, calculated from the variability of the data. Revenue to the processors was then calculated by multiplying the harvest volume by the price.

Revenue to both drift and set gillnet fishermen was estimated using the ex-vessel price and the magnitude of the catch. Ex-vessel price in dollars per kilogram that would be paid in year *y* ($P_{\text{ex},y}$) was estimated using the historic relationship between August Japanese wholesale price and ex-vessel price for the years 1991–2006 (data from Knapp (2004) and G. Knapp, Institute of Social and Economic Research, University of Alaska, Anchorage, AK 99508, USA, personal communication, 2007):

$$(9)\qquad P_{\text{ex},y} = -0.19 + 0.34P_{\text{whole},y} + \varepsilon_{\text{ex},y}$$

Process error ($\varepsilon_{\text{ex},y}$) was assumed to be normally distributed and was simulated by drawing a random normal deviate with a mean of zero and a standard deviation of 0.095 estimated from the data. Again, the average weight of sockeye salmon was assumed to be 2.68 kg and revenue to the fishermen was calculated by multiplying the harvest volume by the ex-vessel price.

The information used for determining the cost of processing and catching fish was obtained directly from appendix F of Link et al. (2003). For their analysis, Link et al. (2003) developed hypothetical processing plants, both shore-based and floating, using information gathered through interviews with plant managers and owners. The floating processor was designed to process crab and Pacific cod, as well as salmon. Because of this, we felt it inappropriate to charge all of the fixed or overhead cost for floating processors to the salmon fishery and subsequently made the assumption that half of the total annual overhead cost would be charged to the Bristol Bay salmon fishery. All other costs for processing salmon described by Link et al. (2003) were included in our model (Table 1).

The operating parameters for the drift and set gillnet fleets were estimated by Link et al. (2003) using information acquired by the State of Alaska Commercial Fisheries Entry Commission for a study designed to determine the optimum number of permits holders for Bristol Bay (Schelle et al. 2004). This information was divided into three groups based on residency: (*i*) residents of the immediate Bristol Bay area, (*ii*) other Alaskan residents, and (*iii*) non-Alaskan residents. Each residency group was further divided into three subgroups based on revenue rankings. We simplified our model by averaging the costs for each revenue group within a residency group, while maintaining the residency stratification (Table 2). For the purpose of simplicity, we elected to use the average residencies by gear group presented by Link et al. (2003). Uncertainty about the cost estimates for both processing and catching fish was not estimated by Link et al. (2003) and consequently was not incorporated into our model.

Gross revenue to the fish processors in year *y* ($I_{\text{proc},y}$) is a function of the magnitude of the catch (C_y), the August Japanese wholesale price ($P_{\text{whole},y}$), and the recovery rate or percentage of the catch converted to marketable product (*r*):

$$(10)\qquad I_{\text{proc},y} = C_y P_{\text{whole},y}\, r$$

Table 2. Parameters used to simulate costs for each permit fished in the drift and set gillnet fisheries (Link et al. 2003).

	Drift gillnet			Set gillnet		
	Local	Other Alaskan	Non-Alaskan	Local	Other Alaskan	Non-Alaskan
Crew parameters						
Average number of paid crew	1.4	1.7	1.7	2.0	2.0	2.0
Average crew share (prop of gross)	0.14	0.13	0.13	0.05	0.05	0.05
Fixed costs						
Fuel, oil, lubricants	$1 451	$1 192	$1 325	$346	$328	$291
Maintenance	$2 360	$1 944	$2 008	$838	$824	$796
Nets	$1 474	$1 218	$1 205	$573	$563	$545
Miscellaneous gear and supplies	$600	$634	$586	$1 092	$1 074	$1 038
Administrative services	$408	$537	$734	$179	$170	$151
Transportation	$1 054	$1 423	$2 296	$0	$501	$1 000
Food	$1 383	$1 009	$1 259	$626	$621	$613
Insurance	$1 608	$1 643	$1 802	$175	$174	$171
Moorage, gear storage, boat haulout	$652	$1 478	$1 477	$165	$160	$150
Property tax	$369	$568	$515			
Vessel license fees	$48	$47	$48	$100	$100	$100
Permit renewal fees	$188	$202	$572	$312	$312	$312
Total fixed cost[a]	$11 595	$11 895	$13 829	$4 406	$4 827	$5 167
Variable costs						
Total crew share (proportion of gross)	0.196	0.221	0.221	0.100	0.100	0.100
Raw fish tax (proportion of gross)	0.020	0.029	0.030	0.050	0.050	0.050
Total variable costs (proportion of gross)[b]	0.216	0.250	0.251	0.150	0.150	0.150

Note: Costs are in US dollars.

[a] Total fixed cost is the sum of all fixed costs.

[b] Total variable cost is expressed as the proportion of gross revenue and is the sum of the proportions for the variable costs.

Total cost to process the catch for a year ($H_{\mathrm{proc},y}$) is a function of the magnitude of the catch and the variable ($V_{\mathrm{proc},y}$) and fixed (F_{proc}) costs of processing, which differ between shore-based ($V_{\mathrm{shore},y}$, F_{shore}) and floating ($V_{\mathrm{float},y}$, F_{float}) processors. Variable cost for processing the catch for year y was estimated by

$$(11)\qquad V_{\mathrm{proc},y} = V_{\mathrm{shore},y}\, p_s + V_{\mathrm{float},y}(1 - p_s)$$

where p_s is the proportion of the catch processed by shore-based plants. Fixed costs were estimated by

$$(12)\qquad F_{\mathrm{proc}} = \frac{G_{\mathrm{tot}} p_s}{G_{\mathrm{shore}}} F_{\mathrm{shore}} + \frac{G_{\mathrm{tot}}(1 - p_s)}{G_{\mathrm{float}}} F_{\mathrm{float}}$$

where G_{tot} is the total processing capacity and G_{shore} and G_{float} are the capacities of the modeled shore-based and floating processors, respectively. The total cost to process the catch for year y was then

$$(13)\qquad H_{\mathrm{proc},y} = V_{\mathrm{proc},y}\, B_y + F_{\mathrm{proc}}$$

Net present value to the fish processors ($\mathrm{NPV}_{\mathrm{proc}}$) for a time period n years in length is

$$(15)\qquad \mathrm{NPV}_{\mathrm{proc}} = \sum_{y=1}^{n} \frac{I_{\mathrm{proc},y} - H_{\mathrm{proc},y}}{(1 + d)^y}$$

where d is the discount rate.

The calculation of net present value to the drift ($\mathrm{NPV}_{\mathrm{drift}}$) and set ($\mathrm{NPV}_{\mathrm{set}}$) gillnet fishermen was similar to the calculations for the fish processors. The differences were (*i*) the use of ex-vessel price in the place of August Japanese wholesale price in the calculation of gross revenue, (*ii*) the determination of both variable and fixed costs using the proportions of local residents, other Alaskan residents, and non-Alaskans rather than the proportion of catch processed by shore-based operations, (*iii*) the inclusion of an average annual capacity estimate for each drift and set gillnet permit in place of processing capacity, and (*iv*) an accounting for the allocation of catch between drift and set gillnet fisheries.

Application to the sockeye salmon fishery of the Egegik District, Bristol Bay, Alaska

Catch and escapement data for sockeye salmon returning to the Egegik District, Bristol Bay, Alaska, were used to illustrate this model. Escapement data were collected annually using counting towers, catch numbers were obtained from fish ticket data, and age data were collected from both the catch and escapement (West 2003).

Data from the 1974 through 2000 brood years were used to estimate the Beverton–Holt spawner–recruit model (eq. 1) using both the more traditional maximum likelihood methodology and a Bayesian model that incorporated the Metropolis algorithm for Markov chain Monte Carlo simulation (MCMC; Gelman et al. 1995; Carlin and Louis 1996). For the MCMC simulation, 500 samples of the model parameters were collected from a 205 000 sample chain. The first 155 000 samples were discarded to allow the model to stabilize and every 100th sample after the first 155 000 was collected, producing 500 MCMC draws of the model param-

Table 3. Priors used to initialize and constrain the Markov chain Monte Carlo used to estimate the Beverton–Holt spawner–recruit model for sockeye salmon, Egegik River, Bristol Bay, Alaska.

Parameter	Prior	Minimum; maximum	Prior σ
α	4.0	0.1; 20.0	10.0
β^a	30 000	2000; 50 000	50 000
σ	1.0	0.0; 2.0	10.0
z	0.20	0.05; 0.90	10.0

$^a\beta$ is in terms of thousands of fish.

eters. The priors used (Table 3) reflected our general thoughts for sockeye salmon production in the Egegik system, as well as Bristol Bay as a whole. The standard deviation for the priors was selected to reflect our uncertainty in the model parameters and to allow the MCMC model to search a wide range of possible parameter values. Minimum and maximum limits were used to keep the parameters within a reasonable range.

The Dirichlet distribution fit to the observed age composition for the Egegik District (Table 4) was used to randomly generate 500 age distributions. Variation in age composition for the simulated salmon returns was modeled by randomly drawing with replacement from the generated age compositions and applying it to a salmon return.

Average yield or catch for a given harvest policy ($\overline{C}_i$) was estimated as the average for a 100-year simulation (k) of the population exposed to the harvest policy for each of the MCMC draws (j).

$$(16)\qquad \overline{C}_i = \frac{\sum_{j=1}^{500}\sum_{k=1}^{100} C^*_{ijk}}{50\ 000}$$

Fourteen percent of the catch for each simulated year was allocated to the set gillnet fishermen, with the remaining 84% going to the drift gillnet fishermen. This allocation is consistent with the present management plan for the Egegik District.

The approximate size of the catch of the other Bristol Bay Districts is required to obtain reasonable estimates of the wholesale and ex-vessel price (eqs. 8 and 9). Our revenue models were constructed using metric tons of sockeye salmon sold from all of Bristol Bay, and the effect of catches from other districts will have a large effect on the expected price for the Egegik catch. We assumed that the catch of the other Districts would remain at approximately the previous 20-year average (16 million fish) and added the simulated Egegik catch for the estimation of revenue to the processors and fishermen. The biomass of the total Bristol Bay catch used for the estimation of salmon prices for each simulated catch was then

$$(17)\qquad B_y = (C_y + 16\ 000\ 000) \times 2.68$$

in which the average weight of Bristol Bay sockeye salmon is assumed to be 2.68 kg.

It was assumed that 75% of the catch for each simulated year would be processed by shore-based processors and that the residency of the fishermen would be the same as that reported in Link et al. (2003). For drift gillnet fishermen, the proportion of local residents was 0.25, other Alaskan residents, 0.25, and non-Alaskan residents, 0.50. For set gillnet fishermen, the proportion of local residents was 0.43, other Alaskan residents, 0.31, and non-Alaskan residents, 0.26.

Table 4. Statistics reflecting the fit of the Dirichlet distribution to the age composition data for sockeye salmon, Egegik River, Bristol Bay, Alaska.

	Age classes			
	1.2	1.3	2.2	2.3
Observed mean	0.078	0.147	0.454	0.295
Theoretical mean	0.099	0.147	0.444	0.310
Observed variance	0.0052	0.0156	0.0306	0.0129
Theoretical variance	0.0089	0.0125	0.0246	0.0214

Net present value for a given harvest policy by processor and fisherman type (i) was estimated by calculating NPV for each 100-year simulation (k) and then averaging across the MCMC draws (j):

$$(18)\qquad \mathrm{NPV}_i = \frac{1}{500}\sum_{j=1}^{500}\sum_{k=1}^{100}\frac{(I_{ijk} - H_{ijk})}{(1+d)^k}$$

where the discount rate (d) was 0.07. Although a formal economic analysis would have examined a wide range of discount rates, we elected to simplify our analysis by examining just one, leaving the more indepth analysis to future researchers. The United States Office of Management and Budget (Circular No. A-94) recommends a discount rate of 0.07 as it approximates the marginal pretax rate of return on an average investment in the private sector in recent years. A 100-year simulation allowed the biological models to approach equilibrium while capturing the vast majority of the net present value.

Results

The Beverton–Holt model was fit to the Egegik River spawner–recruit data using both the traditional maximum likelihood method and a Bayesian model (Fig. 1*a*). The estimated average yield for the Bayesian model was greater for any level of escapement than the maximum likelihood model and suggested that the highest average yields would occur at higher levels of escapement (Fig. 1*b*). The high expected yields obtained from the Bayesian model are due to the uncertainty in the spawner–recruit data set. The data are reasonably consistent with the hypothesis of no density dependence (Fig. 1*a*), and only our maximum prior for β (50 million fish; Table 3) keeps the Bayesian model from including significant weight for this possibility. The maximum likelihood method did not fully account for uncertainty in the data and suggested more evidence for density dependence. A lack of density dependence implies much higher potential yields at all spawning stock sizes.

Evaluation of harvest policies for optimum biological yield

One important model output was the estimation of the range of harvest policies that produce large, sustained catches. Although the maximum average yield for any harvest control

Fig. 1. (*a*) The fit of the Beverton–Holt escapement–recruit curve and (*b*) a comparison of the resulting yield curves using a traditional maximum likelihood fit (broken line) and a Bayesian model (solid line) for sockeye salmon (*Oncorhynchus nerka*), Egegik River, Bristol Bay, Alaska.

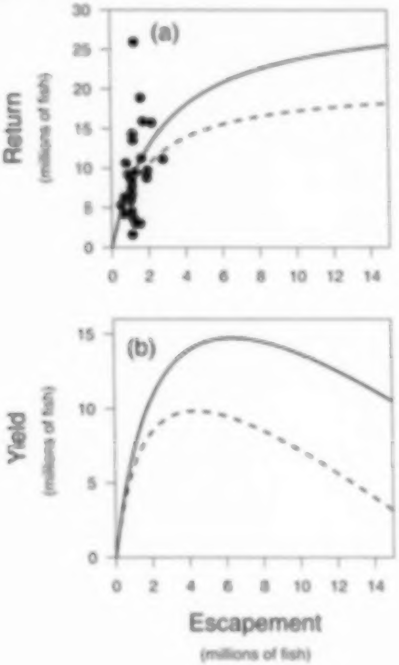
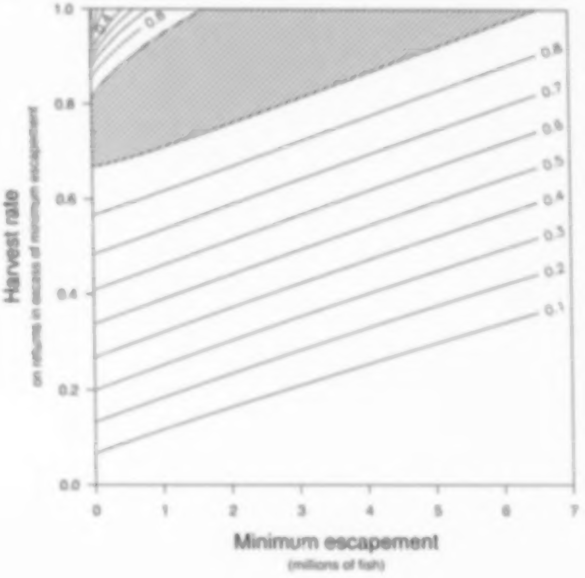


Fig. 2. Estimated proportion of the maximum average biological yield obtained from a wide range of harvest policies for sockeye salmon (*Oncorhynchus nerka*) returning to the Egegik River, Bristol Bay, Alaska. Hatched region represents 90% and greater of the maximum biological yield.



rule examined was just over 12.1 million fish, we found that large sustained catches in excess of 11.0 million fish could be expected for a wide range of control rules.

Biological escapement goals in Alaska are often expressed as the range of escapements most likely to produce a catch that is 90% or greater of the maximum sustained yield or the maximum average catch. In Bristol Bay, this goal is generally obtained using a fixed escapement rule, which is represented in our control rule by setting $u = 1$ (eq. 7). Another commonly used harvest policy is the management for a fixed exploitation rate, which can be viewed as a fixed harvest rate without a minimum escapement goal. Our simulation results indicate that a fixed escapement goal policy with a range of 1.6 to 6.6 million fish or a fixed harvest rate policy with exploitation rates of 0.67 to 0.82 will produce, on average, catches within 90% or greater of the maximum sustained yield (Fig. 2). In addition, there is a wide range of other harvest policies that will produce average yields within 90% of the maximum.

Evaluation of harvest policies for optimum economic yield

We calculated the maximum net present value for the processing sector and the drift and set gillnet fleets by fixing the capacity of those segments of the industry and then searching for the harvest control rule that maximizes the net present value (Fig. 3). For all industry components examined, there is a capacity that maximizes net present value, roughly 10 million fish for processors, 12 million fish for drift gillnetters, and 2.1 million fish for set gillnetters. Capacity is directly related to the size of the processing plant or the magnitude of the individual fishing operation and ultimately reflects the level of fixed costs required to process or harvest fish. In general, processors and fishermen are undercapitalized and unable to catch or process the available catch for the ascending or left side of the curve, while they are overcapitalized and do not make efficient use of their investment in capacity for the right side or descending limb. The number of processors or the number of fishermen that optimize NPV can be estimated by finding the capacity for which NPV is maximized and dividing it by the average processor size or average drift or set gillnet capacity.

We explored a range of minimum escapements and harvest rates along with optimum capacity of the processors and fishing fleets for economic yield to see how economic performance varied with the control rule. As with the biological yield analysis, we found a wide range of harvest policies likely to produce high, sustained economic returns (Fig. 4).

Comparison of harvest policies for optimizing biological and economic yield

A comparison of the harvest policies that optimized biological and economic yield was performed by combining the results of the biological and economic evaluations and visually comparing them (Fig. 5). Net present value was optimized for harvest policies that could be considered more aggressive than those that optimized biological yield. Portions of the range of minimum escapements that optimized NPV were lower than those that optimized biological yield. Likewise, the range of harvest rates that optimized NPV was wider and completely encompassed the range that optimized biological yield.

Fig. 3. Estimated relationship between net present value and maximum capacity for the processors (broken line) and the drift (thick solid line) and set (thin solid line) gillnet fleets, Egegik River, Bristol Bay, Alaska.

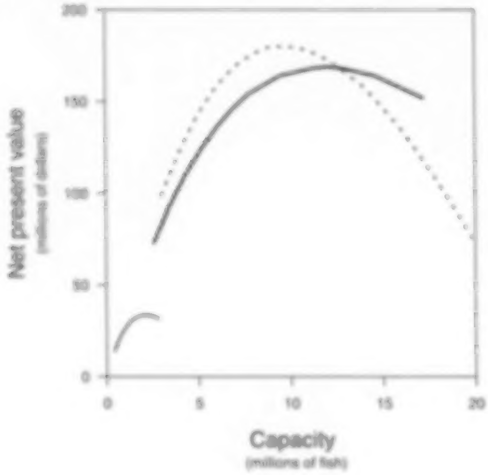
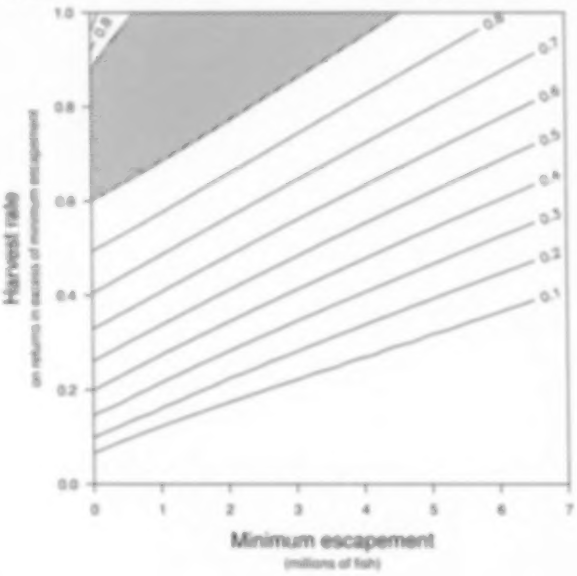


Fig. 4. Estimated proportion of the maximum average net present value for the drift gillnet fleet obtained from a wide range of harvest policies for sockeye salmon (*Oncorhynchus nerka*) returning to the Egegik River, Bristol Bay, Alaska. Hatched region represents 90% and greater of the maximum net present value.



Discussion

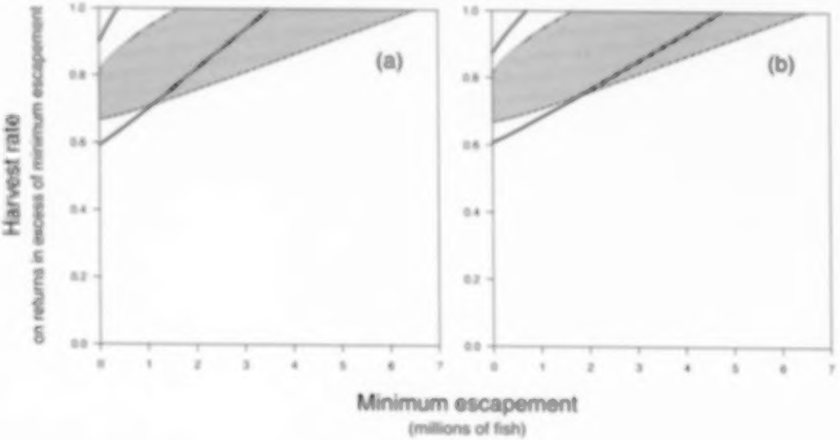
Our method of computing the escapement goal range that maximizes biological yield (also known as the biological escapement goal or BEG) adds a number of factors that have not been considered in past Bristol Bay BEG analyses, but it does not provide a qualitatively different picture of optimum biological management. In general, the range of escapements that would emerge as the formal escapement range under the 90% of MSY rule would be broader and, in particular, go to higher values of escapement than the traditional Beverton–Holt fitting. The broader range is partially due to considering parameter uncertainty in the Bayesian analysis. For these methods, large escapements tend to produce larger than average salmon returns because of the assumption of a lognormal error structure. If you have a large escapement and unusually good recruits per spawner, then you will get a very large salmon return, which greatly affects the overall average.

Consideration of salmon price, the cost of harvesting and processing fish, and processing and harvesting capacity provides a very different view of "optimal" management. The most striking effect was the importance of capping capacity: it simply does not pay to have a large fishing fleet or processing capacity that is only used every few years. This has been recognized by the Commercial Fisheries Entry Commission in its recommendations for a much smaller fleet, and the processing industry has certainly reduced its capacity in recent years. It would seem appropriate for the official harvesting policy to recognize that the economic viability of the industry may be enhanced if there was a maximum catch limit for the Bay. The August Japanese wholesale and ex-vessel price relationships are sensitive to changes in the worldwide demand for wild Bristol Bay sockeye salmon. Accurate estimates of these price relationships are critical for determining of the optimal management policy and capacity cap to maximize future economic benefits.

Capping catch implies that in years of large salmon returns, there will be some large escapements to individual river systems. Although the Kvichak River has had escapements in excess of 20 million fish, there are concerns that an escapement of 3–10 million fish in any of the other Bristol Bay River systems might have an impact on future spawning success and juvenile fish growth. Before formally adopting harvest strategies that incorporate a maximum catch component, a biological evaluation that examines both the risks of large escapements on future salmon production and the benefits of large escapements to a wide range of other ecosystem components such as nutrient inputs, primary production, resident freshwater fish species, and terrestrial animals should be considered (Cederholm et al. 1999; Hilderbrand et al. 1999; Schindler et al. 2005). The recent large escapements in the Alagnak River and Wood River systems of Bristol Bay will provide useful information for this evaluation (Schindler et al. 2006; Quinn et al. 2007).

The impact of volume on price appears to primarily affect the harvesting strategy at low run sizes, and our analysis suggests that the bottom end of the escapement range should be a "soft landing" rather than a "hard floor". When salmon returns are low and the price is high, it is economically optimal to allow some harvesting, even at low stock sizes. It is important to note that this applies only to Bristol Bay wide catch. If an individual district has a poor salmon return but the other districts have good salmon returns, then the total Bristol Bay wide production will not be low, the price will not be particularly high, and there will be no economic ben-

Fig. 5. Estimated biological yield (hatched area) and net present value (heavy lines) for (*a*) the fish processors and (*b*) the set gillnet fishermen obtained from a wide range of harvest policies for sockeye salmon (*Oncorhynchus nerka*) returning to the Egegik River, Bristol Bay, Alaska. The hatched area indicates the region of 90% and greater of the maximum biological yield; the solid lines indicate the outline for the region in which 90% and greater of the maximum net present value was obtained.



efit for harvesting below the escapement floor in the weak district.

Although all of our analyses are built on the assumption of a single annual harvest decision, in practice these stocks are managed in-season, and the harvesting and processing capacities are daily limits rather than annual limits. It would be useful to evaluate the in-season implementation of harvest strategies to determine if there are ways to provide for more early-season harvest. Early-season harvest has the potential of improving the economics by allowing a fixed capacity in both the harvesting and processing sectors to handle more fish through a single season. Bristol Bay managers are traditionally reluctant to provide much fishing opportunity until they are confident that they will reach their escapement goals. The results of the economic analysis suggest that some harvesting below traditional escapement floors is economically optimal, thus the economic performance of the fishery may be enhanced by more aggressive fishing early in the season.

We see several avenues for further work on harvest strategies. We have shown that the optimal harvest strategy with economic objectives can differ significantly from the biological escapement goal. We used published economic data but suggest that an updating of the data is in order, and a more in-depth economic analysis, including a detailed examination of our assumption regarding the economic discount factor, should be made. Although the cost of fishing and fish processing have most likely been affected by the recent increase in the price of petroleum products, it is also highly likely that the salmon price-to-volume relationships are in flux because of changing world markets. The integration of the annual harvest strategy with the reality of in-season management is a high priority. A major limitation of the methods used here is the use of brood tables to summarize the life history of the fish. The biology of sockeye salmon has shown great changes in survival over different life history stages, and it seems likely that an analysis based on a life history model, including freshwater and marine survival, would provide a better understanding of the role of density dependence in these stocks and, indeed, in almost all salmon.

Finally, it would be useful to calculate the optimal harvest strategies simultaneously for all fishing districts. Bristol Bay harvest strategies have traditionally been evaluated on a district-by-district basis, but the harvesting and processing capacity and impacts of volume on price are a Bristol Bay wide phenomena. Although this is not a trivial task, we suspect that it is now possible with modern computational methods and should be pursued.

Acknowledgements

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Effects of solar ultraviolet radiation on the behaviour of juvenile coho salmon (*Oncorhynchus kisutch*): avoidance, feeding, and agonistic interactions

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Abstract: The behaviour of juvenile coho salmon (*Oncorhynchus kisutch*) was observed in outdoor experimental flumes in which three different spectral regimes were created by plastic covers that selectively blocked all or portions of natural ultraviolet radiation (UVR). The three light treatments were (*i*) photosynthetically active radiation (PAR, 400–700 nm), (*ii*) PAR plus longer wavelength ultraviolet (PAR + UVA, 320–700 nm), and (*iii*) full-spectrum sunlight with both long and short wavelength ultraviolet included (PAR + UVA + UVB, 280–700 nm). Observations made at different times of the day and under both overcast and sunny skies allowed an assessment of PAR intensity on behaviour in addition to that of UVR. We quantified shade-seeking behaviour, feeding strikes, and agonistic interactions (approaches, chases, and nips) between individuals. Under higher PAR intensities, a greater proportion of juvenile coho tended to take cover under rocks. Shade-seeking behaviour increased significantly in the presence of UVR. Feeding and agonistic interactions were partially inhibited at higher PAR intensities and very significantly depressed by UVR. For all behaviours tested, the effects were mediated by UVA with no significant additional impacts from UVB. UVR-mediated effects on behaviour could have ecological consequences through influencing summer densities, density-dependent growth, and size-dependent winter and early marine survivals.

Résumé : Nous avons observé le comportement de jeunes saumons coho (*Oncorhynchus kisutch*) dans des canalisations expérimentales érigées à l'extérieur et dans lesquelles trois régimes spectraux ont été aménagés à l'aide de couvertures plastiques qui bloquent de façon sélective une partie ou l'ensemble de la radiation ultraviolette (UVR) naturelle. Les trois traitements lumineux consistaient en (*i*) une radiation active pour la photosynthèse (PAR, 400–700 nm), (*ii*) PAR plus l'ultraviolet à grandes longueurs d'onde (PAR + UVA, 320–700 nm) et (*iii*) le spectre complet de la lumière solaire y compris l'ultraviolet de courtes et grandes longueurs d'onde (PAR + UVA + UVB, 280–700 nm). Des observations menées à différents moments de la journée et dans des conditions d'ensoleillement et de nébulosité ont permis d'évaluer l'influence de l'intensité de PAR sur le comportement, en plus de celle de l'UVR. Nous avons mesuré le comportent de recherche d'ombre, les attaques alimentaires et les interactions agressives (rapprochements, poursuites et morsures) entre les individus. Aux intensités plus élevées de PAR, une plus grande proportion des jeunes saumons coho a tendance à se réfugier sous les pierres. Le comportement de recherche d'ombre s'intensifie significativement en présence d'UVR. L'alimentation et les interactions agressives sont partiellement inhibées aux intensités plus élevées de PAR et sont très significativement réduites par l'UVR. Pour tous les comportements testés, les effets sont provoqués par l'UVA, sans impact additionnel significatif de l'UVB. Les effets provoqués par l'UVR sur le comportement pourraient avoir des conséquences écologiques en influençant les densités en été, la croissance dépendante de la densité et la survie dépendante de la taille en hiver et au début du séjour en mer.

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Introduction

Most of the studies on ultraviolet radiation (UVR) and fish have been of three general types: effects of UVR on fish health and physiology, behavioural responses of fish to UVR (i.e., UVR avoidance), and the uses made by fish in foraging, navigation, and communication. The most researched area has been the effects of UVR on fish health and physiology. The deleterious effects on fish of exposure to UVR have been known for many years (Crowell and McCay 1930; Bell and Hoar 1950) and are well documented (Browman et al. 2000; Whitehead et al. 2000; Zagarese and Williamson 2001). It is well established that UVR is particularly damaging to fish larvae (e.g., Béland et al. 1999;

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Zagarese and Williamson 2001), and lethal effects have been demonstrated for diverse species (e.g., Charron et al. 2000; Steeger et al. 2001; Häkkinen et al. 2003). Effects on larger fish are usually sublethal and include ocular damage (Cullen and Monteith-McMaster 1993), skin lesions (Bullock 1988), and the suppression of immune responses (Salo et al. 1998) and metabolic rates (Winckler and Fidhiany 1999). Many fish species that are exposed to UVR in their natural habitats have protective chemical and cellular mechanisms that prevent or repair cellular and molecular damage caused by UVR. For example, salmonids, which commonly occur in the shallow fresh waters of temperate regions and are therefore prone to UVR exposure, have a facultative chemical UVR screen (Fabacher and Little 1995; M.L. Bothwell, unpublished data).

Because UVR is potentially damaging, behavioural responses have evolved that enable fish to avoid or reduce UVR exposure (Leech and Johnsen 2003). For example, juvenile coho salmon (*Oncorhynchus kisutch*; Kelly and Bothwell 2002), vendace (*Coregonus albula*), and whitefish (*Coregonus lavaretus*; Yloenen et al. 2004), all of which occur in shallow, temperate fresh waters where UVR levels are high, have been shown to actively reduce their exposure to UVR by hiding. In coho salmon, such avoidance is specific to UVR and is not simply an avoidance of light (Kelly and Bothwell 2002). Yellow perch (*Perca flavescens*) spawn at different depths in temperate lakes with different dissolved organic carbon (DOC) concentrations to reduce exposure of their eggs and larvae to UVR (Huff et al. 2004).

Although there is little doubt that excessive exposure to UVR can be harmful to fish, there is also evidence that fish exploit this facet of their photic environment. For example, the roles that UVR might play in fish foraging have been widely investigated (Browman et al. 1994; White et al. 2005; Leech and Johnsen 2006), and UVR is likely used in oceanic migration (Waterman 2006) and in intraspecific communication in fishes (Smith et al. 2002; Cummings et al. 2003; Siebeck 2004).

The present study is, to our knowledge, the first to consider indirect effects of UVR on intraspecific social interactions that are the consequence of UVR avoidance. Coho salmon, like all *Oncorhynchus* spp., are anadromous. After hatching and emerging from the gravel in early spring, juvenile coho salmon spend about a year in fresh water before entering the ocean (Sandercock 1991). While in fresh water, juvenile coho act aggressively towards conspecifics and typically form dominance hierarchies in which the dominant fish occupies the most energetically favourable feeding position (Fausch 1984; Glova 1986; Holtby et al. 1993). Agonistic interactions and the resultant spacing between individuals are thought to limit rearing densities (Chapman 1962; Mason and Chapman 1965; Grant and Kramer 1990). The modalities of the agonistic interactions have been well studied and involve both visual and physical contact between individuals (Dill 1978; Swain and Riddell 1990; Holtby et al. 1993). We reasoned that when juvenile coho avoid UVR by hiding, visual and physical contact between individuals would be reduced and a reduction in the number and intensity of agonistic interactions would result.

Materials and methods

Mesocosom flume design

The behaviour of juvenile coho was observed in a set of outdoor experimental flumes located on an unshaded bank of the Little Qualicum River, Vancouver Island, British Columbia. The mesocosm-scale flumes were designed to study the effects of solar ultraviolet radiation on stream biotic communities that included juvenile coho.

The flumes (240 cm long × 30 cm wide × 20 cm high) were constructed of UV transparent acrylic (OP-4 Acrylite; CYRO, Rockaway, New Jersey), aligned north to south and arranged in parallel with 60 cm spacing between adjacent troughs. This spacing and the clear plastic sides enabled visualization of the juvenile coho in all the flumes.

The three light treatments were created by covering the flumes with one of the following light transmitting plastics. (*i*) Flumes exposed to photosynthetically active radiation (PAR, 400–700 nm) alone were covered with OP-2 Acrylite (CYRO, Rockaway, New Jersey), which allows ~90% of PAR to pass, while blocking ~94% of the UVA (320–400 nm) and 100% of the UVB (290–320 nm) (Fig. 1). (*ii*) PAR + UVA (320–700 nm) treatments used 0.1 mm thick Mylar-D sheeting (DuPont, Wilmington, Delaware). Mylar-D allows ~85% of PAR and ~75% of the UVA to pass, while blocking ~80% of UVB (Fig. 1). (*iii*) PAR + UVA + UVB (280–700 nm) treatments used OP-4 Acrylite (CYRO), which allows ~93%, 90%, and 75% of the PAR, UVA, and UVB, respectively, to pass (Fig. 1). Each of the three light treatments (PAR, PAR + UVA, and PAR + UVA + UVB) was run in triplicate for a total of nine flumes. The three light treatments were randomized within each of three groups of three flumes. The rigid plastic solar screens (OP-2 and OP-4) extended 10 cm beyond all sides of the flumes. The flexible, Mylar-D sheeting was draped over each of the flumes in the PAR + UVA treatment so that it covered the top and both long sides of the flumes, blocking most diffuse radiation. These precautions in conjunction with a 20 cm fish-free zone at the southerly facing, foot end of the flumes restricted unwanted wavelengths of direct sunlight from impinging on the flumes at all but the lowest sun angles.

Two, 50 cm long riffle zones were created in each flume by lining areas of the bottom with paving bricks and placing 21 stones (5–6 cm diameter) on top of the bricks. Water depth in the riffle zones was ~7 cm. Two deeper pool areas in each flume (50 cm long and ~14 cm deep) contained three large rocks (11–12 cm diameter) that provided juvenile coho with refuge from current, potential shade, and the possibility of visual isolation from other fish.

All stones and rocks placed in the flumes were taken from the nearby river and had well-established algal and insect communities. Invertebrate production in situ along with the continuous inflow (100 $L \cdot min^{-1}$) of unfiltered water pumped from the river through each flume allowed the coho to forage naturally during the 55-day experimental period.

Juvenile coho used in the trial were gathered by pole seine from the Little Qualicum River. The fish collected were anaesthetized, weighed, and measured. Coho between 2.0–2.5 g and 5.8–6.3 cm fork length were selected for the experiment. At random, five individual coho were placed into

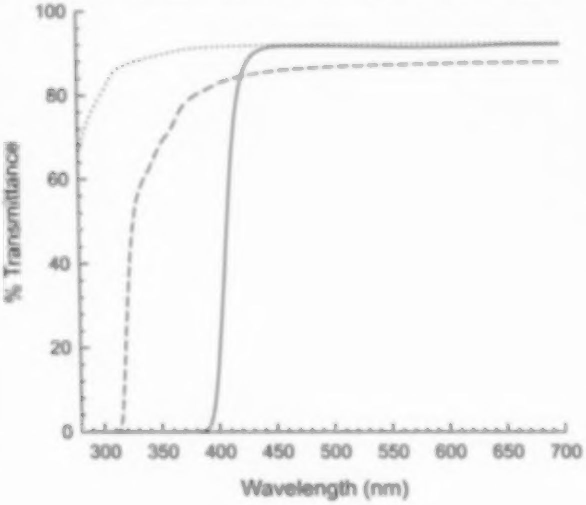


Fig. 1. Transmission spectra of the plastic covers used to create different photic environments. OP-4 Acrylite transmitted full-spectrum sunlight (PAR + UVA + UVB; dotted line), Mylar-D film blocked UVB wavelengths (PAR + UVA; broken line), and OP-2 Acrylite blocked all ultraviolet wavelengths (PAR; solid line).

each of the nine flumes for a stocking density of ~8 fish·m^{-2}. Coho were confined by plastic screens and perforated baffles at the head and foot ends of each flume but were free to move between pool areas.

Behavioural observations

Behavioural observations began approximately four weeks after the fish were put into the flumes. Observations were made on five days during a three-week period in July and August 2000. To accommodate different overall light intensities, observations were made at different times of the day between 0850 and 2040 and under conditions of both overcast and sunny skies. On each observation day, behaviour was recorded for 15 min in each of the nine flumes. This gave a total of 15 replicated observation periods for each of the three UV environments (three replicated flumes per spectral environment × five observation days).

Screening the flumes to visually isolate the observer and the flumes proved impractical. Instead, the observation protocol was designed to minimize disturbance. Observations on a flume were made at a distance >2.5 m. For the first two flumes in the row, observations were made at a distance of 3–4 m, and for the remaining flumes, observations were made with two intervening flumes, which had already been observed. After moving into position, the observer waited 5 min before the trial began. During this acclimation period, all of the visible coho in the flume were located. Sudden or excessive movements were avoided, and the observer was careful not to cast shadows onto flumes that had not been observed. Handheld counters and timers were used, so for 20 min after moving into position, the observer was essentially motionless. At the end of each day's observations, a close examination of each of the flumes was made to determine the number of coho that could be found in each. The number of authenticated residents was recorded as coho SEEN.

Three categories of behaviour were reported: (*i*) photoavoidance and cover seeking, (*ii*) feeding strikes, and (*iii*) intraspecific agonistic interactions. Photoavoidance and cover seeking was assigned to individuals hiding under rocks but still visible to the observer from the side of the flume from which observations were made. These fish were designated as HIDDEN (Fig. 2*a*) and distinguished from EXPOSED individuals swimming in open water of the flumes (Fig. 2*b*). The number of fish SEEN occasionally exceeded the number HIDDEN + EXPOSED. Feeding strikes were tallied for biting motions directed at food items in the drift. Agonistic interactions were subdivided into three types: (*i*) an approach, a distinct movement toward another fish, whether by active swimming or passive drifting (Kratt and Smith 1979); (*ii*) a chase, a prolonged approach or charge by an aggressor and flight by the chased fish from its original position; and (*iii*) a nip, a biting motion toward a second fish, either attempted (i.e., the threat nip of Chapman 1962) or achieved. These last three aggressive interactions were summed and used as a measure of total aggressive activity. The number and duration of lateral displays (Chapman 1962; North 1979; Swain and Holtby 1989) would have been noted as well, but none was observed during this experiment. During each 15 min observation period, the total time in which fish were engaged in aggressive interactions was noted to the nearest second.

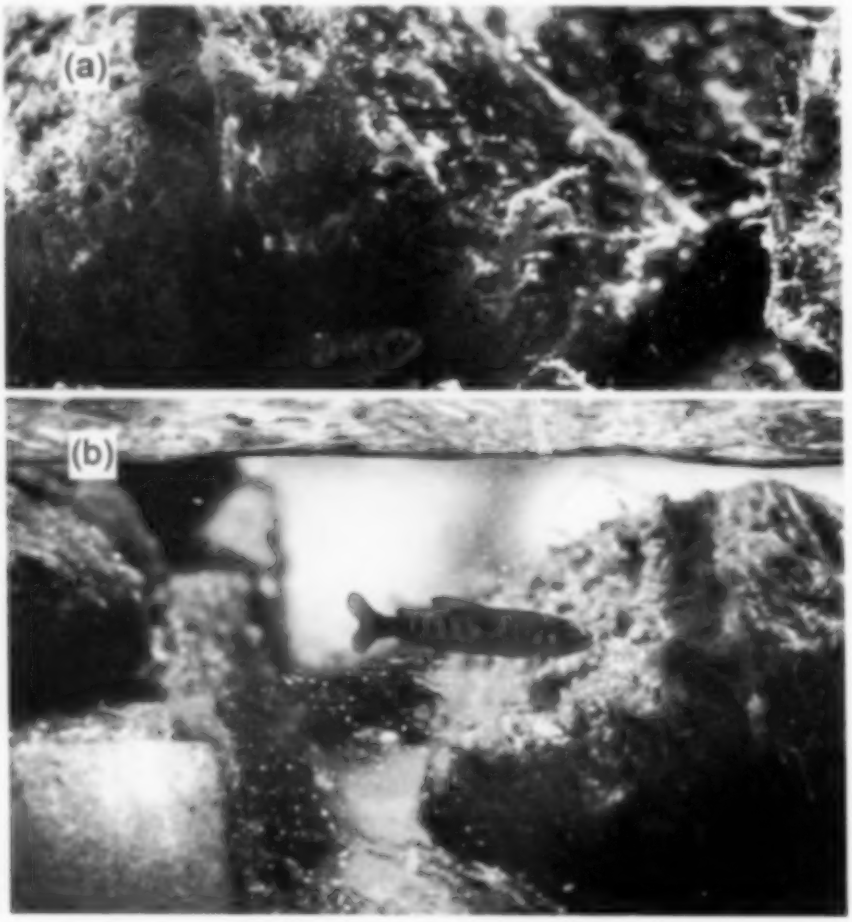
Light data

During the experiment, hourly integrals of photosynthetically active radiation (PAR) incident on the site were recorded using an integrating light meter (LI-550B; LiCor, Lincoln, Nebraska) and a quantum sensor (LI-190SB; LiCor). Spectral scans of the transmission of the optical filters placed over the flumes were used to adjust these values to PAR flux (E·m^{-2}·h^{-1}) impinging on the water surface in the flumes during hours of observation.

Data management and statistical analysis

The number of EXPOSED fish and the total observed numbers of feeding strikes and all agonistic interactions in each flume were standardized to the number of authenticated (SEEN) individuals and then normalized by log transformation (after adding 1.0). Data were analyzed by analysis of covariance (ANCOVA; Sokal and Rohlf 1995, pp. 499–521) as implemented in SYSTAT (version 11; Wilkinson and Coward 2004). Initially, two-way ANCOVA, with light treatment and flumes (nested within the light treatments) as the effects and with PAR flux and either the number of visible fish (HIDDEN + EXPOSED) or the number of SEEN residents as covariates, was used to determine the effects of light quality on behaviours. The models with SEEN fish as a covariate consistently showed significantly better fit (higher explained variance as measured by R^2 and lower mean squared error (MSE)). Homogeneity of slopes for both covariates for each dependent variable was confirmed by estimating the dependent × covariate interaction terms. Finally, no flume effects were detected in any of the analyses, so the results reported are for a one-way ANCOVA with light treat-

Fig. 2. Juvenile coho in (*a*) a HIDDEN position under a rock in the central pool of a flume exposed to PAR + UVA and (*b*) an EXPOSED position in the central pool of a flume shielded from UVR (PAR alone). These positions were typical for individuals in the two light treatments during the day. The dates of observation were 19 and 26 July (days 200 and 207) and 2, 6, and 12 August (days 214, 218, and 224).



ment as the effect and PAR flux and the number of SEEN fish as covariates with the following model:

$$(1)\qquad Y_{ij} = \mu + \alpha_i + \beta_{\text{within}}(X_{ij} - \bar{X}_i) + \beta'_{\text{within}}(X'_{ij} - \bar{X}'_i) + \varepsilon_{ij}$$

where Y_{ij} is the *j*th observation in the *i*th light treatment; μ is the grand mean; α_i is the fixed treatment effect for light treatment *i*; β_{within} and β'_{within} are the pooled, within light treatment slopes of the regression of variable *Y* on the covariates *X* and *X*', respectively; and ε_{ij} is the random deviate.

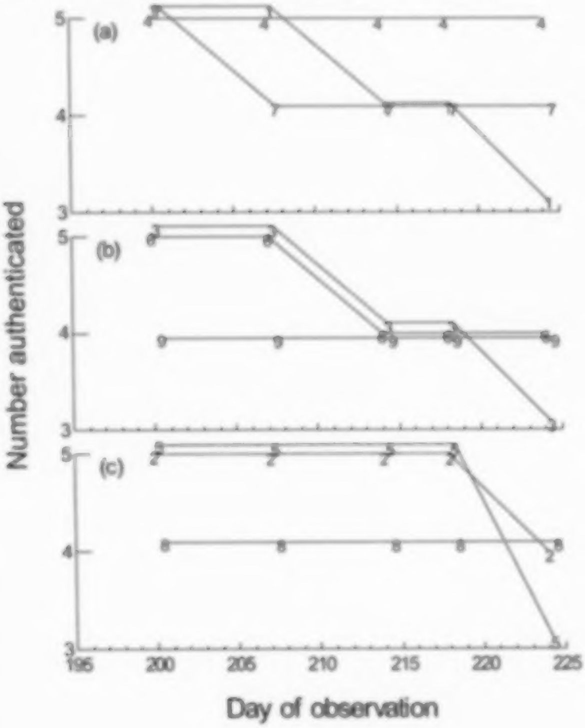
Results

On all of the observation days, coho appeared to be missing from at least one flume, i.e., they could not be located even on close inspection. On our first day of observation, five fish were present in seven of nine flumes and four were present in the other flumes. On the last day of observation, only one flume had five fish, whereas five had four and three had three fish (Fig. 3). The number of coho missing showed no relationship to light treatment or to the light intensity at the time of observation.

Shade-seeking behaviour

The proportion of fish in exposed positions (i.e., open water) was affected by both light intensity and the presence of UVR. Fish were significantly more likely to be in open water at low light intensities ($P < 0.05$; Table 1; Fig. 4) and in the absence of UVR ($P < 0.01$; Table 1). The positions of fish in flumes exposed to UVR were often markedly different from those in flumes exposed only to PAR particularly in midday under clear sky (e.g., Fig. 2). The proportion of exposed fish was smaller in the PAR + UVA + UVB light treatment than in the PAR + UVA treatment (i.e., $\alpha_{\text{PAR+UVA+UVB}} < \alpha_{\text{PAR+UVA}}$; Table 1), but post hoc tests showed that the difference was not significant ($P > 0.05$; Table 1). No significant effect of density was observed (Table 1), suggesting that the flumes had sufficient cover for all fish seeking it.

Fig. 3. The number of authenticated coho (SEEN) in each flume over the experimental period. The observations have been grouped by light treatment: (*a*) PAR; (*b*) PAR + UVA; and (*c*) PAR + UVA + UVB. The numbers are the flume numbers. Some of the numbers and connecting lines have been offset for clarity.



Feeding behaviour

The number of feeding strikes per fish tended to decline with increasing light intensity, but the relationship was not significant ($P = 0.17$; Table 2; Fig. 5). No density effects were observed (Table 2). However, there was a weak tendency for number of feeding strikes per fish to be lower in the presence of UVR (post hoc test 1, $P < 0.05$; Table 2). The number of feeding strikes was lower in the PAR + UVA + UVB light treatment than in the PAR + UVA treatment, but the difference was not significant (post hoc test 2, $P > 0.05$; Table 2).

The feeding strikes that did occur in the presence of UVR were typically quite different from those that occurred with PAR illumination only. A feeding strike for a HIDDEN fish in a UVR-exposed flume usually involved a dash to the detected item, a strike, and an equally rapid return to cover. A feeding strike for an EXPOSED fish in the absence of UVR was less hurried, and a return to station often comprised a backward and downward drift, not a dash.

Fig. 4. The proportion of fish that were EXPOSED (of the number authenticated) as a function of PAR flux and light treatment (□ and dotted line, PAR + UVA + UVB; + and broken line, PAR + UVA; ● and solid line, PAR). The lines are linear regressions within photic treatments.

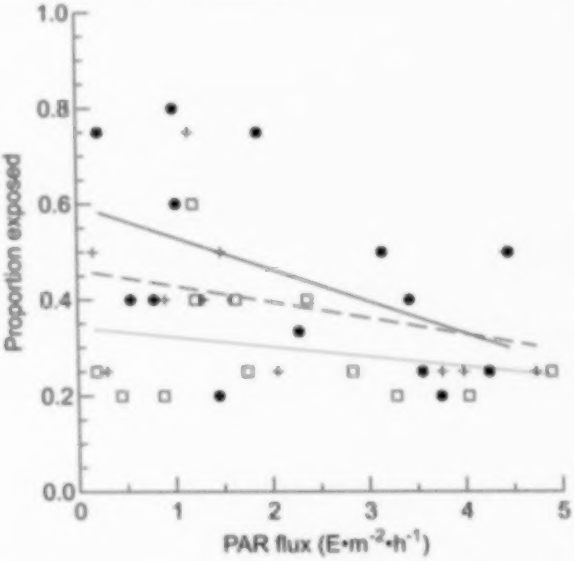
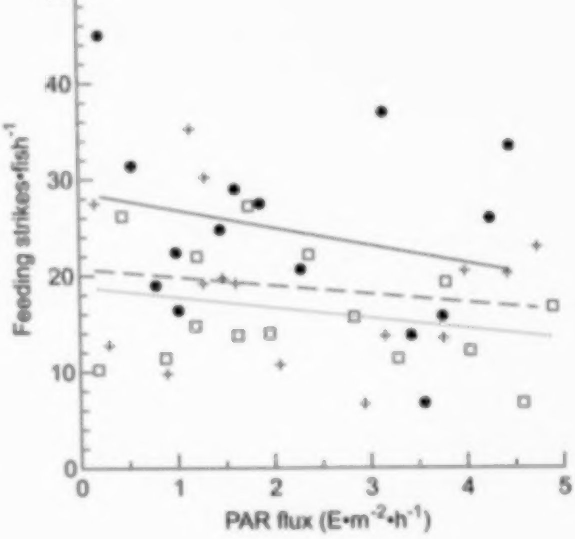


Fig. 5. The number of feeding strikes per fish SEEN as they varied with PAR flux and light treatment (□ and dotted line, PAR + UVA + UVB; + and broken line, PAR + UVA; ● and solid line, PAR). The lines are linear regressions within photic treatments showing nonsignificant reductions in the number of strikes as PAR flux increased ($P > 0.10$).



Agonistic behaviours

Two of the three aggressive interactions between individual coho (approaches and chases) and the sum of the three interactions when expressed on a per fish basis were significantly ($P < 0.01$) reduced by light intensity (PAR flux; Figs. 6*a*–6*d*). Agonistic interactions tended to increase with density (Table 3, variables *a*–*d*), but this effect was only significant for nips ($P < 0.05$; Table 3, variable *c*). The pres-

Table 1. Summary of the analysis of covariance (ANCOVA) analysis related to photoavoidance.

Model parameter (eq. 1)	μ	$\beta_{\text{within PAR flux}}$	$\beta'_{\text{within SEEN}}$	α_{PAR}	$\alpha_{\text{PAR+UVA}}$	$\alpha_{\text{PAR+UVA+UVB}}$
Parameter estimate	0.157	–0.034	0.046	0.073	0.0055	–0.079
Tests of main effects		$F_{[1,40]}$ = 5.72*	$F_{[1,40]}$ = 1.89 NS	$F_{[2,40]}$ = 5.43**		
Post hoc test 1: PAR > (PAR + UVA and PAR + UVA + UVB)	$F_{[1,40]}$ = 7.47**					
Post hoc test 2: PAR + UVA = PAR + UVA + UVB		$F_{[1,40]}$ = 3.19 NS				

Note: Dependent variable, log(proportion + 1) of authenticated fish in an exposed position; covariates, photosynthetically active radiation (PAR) flux ($E \cdot m^{-2} \cdot h^{-1}$) and the number of authenticated coho (SEEN). Post hoc test 1 considers whether the adjusted mean of the dependent variable in the PAR light treatment is equal to the pooled adjusted means of the other light treatments. Post hoc test 2 considers whether the adjusted means of the dependent variable in the PAR + UVA and PAR + UVA + UVB light treatments are equal. Probability levels for hypothesis tests are indicated: NS, $P > 0.05$; *, $P \leq 0.05$; **, $P \leq 0.01$.

Table 2. Summary of the analysis of covariance (ANCOVA) analysis related to feeding strikes.

Model parameter (eq. 1)	μ	$\beta_{\text{within PAR flux}}$	$\beta'_{\text{within SEEN}}$	α_{PAR}	$\alpha_{\text{PAR+UVA}}$	$\alpha_{\text{PAR+UVA+UVB}}$
Parameter estimate	3.17	–0.063	–0.017	0.208	–0.053	–0.155
Tests of main effects		$F_{[1,40]}$ = 1.91 NS	$F_{[1,40]}$ = 0.023 NS	$F_{[2,40]}$ = 3.14 NS		
Post hoc test 1: PAR > (PAR + UVA and PAR + UVA + UVB)	$F_{[1,40]}$ = 5.75*					
Post hoc test 2: PAR + UVA = PAR + UVA + UVB		$F_{[1,40]}$ = 0.45 NS				

Note: Dependent variable, log(number of observed feeding strikes + 1) per fish SEEN; covariates, photosynthetically active radiation (PAR) flux ($E \cdot m^{-2} \cdot h^{-1}$) and the number of authenticated coho (SEEN). The format of the table is described in the caption to Table 1. Probability levels for hypothesis tests are indicated: NS, $P > 0.05$; *, $P \leq 0.05$.

ence of UVR significantly suppressed agonistic behaviour ($P < 0.05$; Table 3, variables *a*–*d*). Although all agonistic behaviours were less numerous in the PAR + UVA + UVB light treatment than in the PAR + UVA treatment (i.e., $\alpha_{\text{PAR+UVA+UVB}} < \alpha_{\text{PAR+UVA}}$; Table 3, variables *a*–*d*), post hoc tests suggested that there were no significant differences between the two light treatments (post hoc test 2, $P > 0.05$; Table 3, variables *a*–*d*).

Light intensity, light quality, and density all affected the time spent per fish in agonistic behaviours. Fish spent significantly more time interacting at low light intensities ($P < 0.01$; Table 3, variable *e*) and in the absence of UVR ($P < 0.01$; Table 3, variable *e*) but more time interacting at higher densities ($P < 0.05$; Table 3, variable *e*). The presence of UVA significantly reduced the time spent by an individual in agonistic behaviours ($P < 0.01$; Table 3, variable *e*), but the difference between the PAR + UVA + UVB and PAR + UVA light treatments was not significant (post hoc test 2, $P > 0.05$; Table 3, variable *e*).

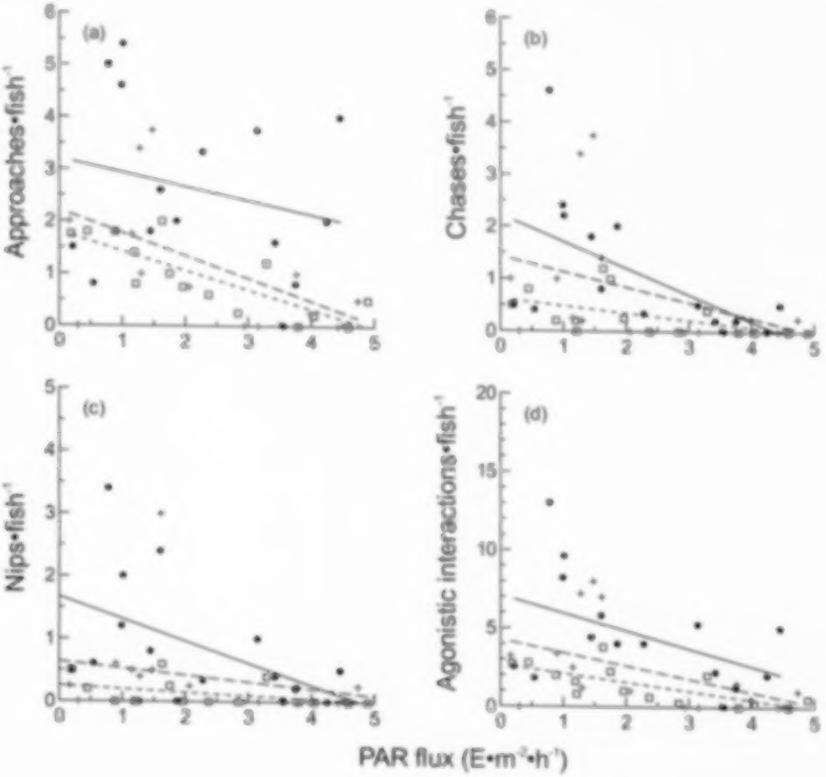
The reductions in time spent in agonistic behaviours largely were due to reduced number of interactions and not to any changes in the average duration of behaviours. The average duration of an interaction tended to be shorter at higher light intensities and at lower densities but not significantly so, and there were no effects due to the light treatment ($P > 0.05$ for all; Table 3, variable *f*).

Discussion

Juvenile coho exposed to UVR hid under or between rocks, made fewer feeding strikes, and had fewer agonistic interactions than individuals not exposed to UVR. The duration of single interactions did not differ between the light treatments, so the total amount time involved in agonistic interactions was also significantly lower in the presence of UVR. The addition of UVB radiation to UVA seemed to further suppress all of the agonistic interactions and the mean duration of those interactions, but never significantly so. Juvenile coho and other salmonids cannot see UVB (Hawryshyn and Hárosi 1994; Parkyn and Hawryshyn 2000) and probably do not respond to its presence (or absence), so it is unlikely that this was an effect of UVB. However, because of the characteristics of the UVR exclusion filters that we used, fish exposed to PAR + UVA + UVB actually received approximately 18% higher levels of UVA than those shielded from UVB (i.e., PAR + UVA) (Kelly and Bothwell 2002), and we suspect that those increased levels of exposure to UVA led to the apparent effects of UVB.

There are several possible mechanisms by which UVR could suppress agonistic interactions. The histological damage caused by UVR is well known, and it is possible that the fish exposed to UVR were disinclined to interact because they were not healthy. We cannot definitively exclude this possibility. However, we did not observe any obvious damage to the skin or eyes (Cullen and Monteith-McMaster 1993; Blazer et al. 1997; Nowak 1999) of the fish in any of the flumes, and there were no external fungal infections (Fabacher and Little 1996). Measurements of weight and condition made at the end of the experiments did not indicate differences due to UVR exposure that were consistent with behavioural responses (M.L. Bothwell, unpublished

Fig. 6. The number of (*a*) approaches, (*b*) chases, (*c*) nips, and (*d*) total agonistic interactions as they varied with PAR intensity and light treatment (☐ and dotted line, PAR + UVA + UVB; + and broken line, PAR + UVA; ● and solid line, PAR). The solid lines are linear regressions within photic treatments that show significant reductions in the number of single and combined behaviours as PAR flux increased ($P < 0.05$).



data). The interactions between the fish also appeared to be qualitatively the same under the different light treatments, with no indications of lethargy or ill health in the UVR-exposed fish. In summary, we think it unlikely that the fish exposed to UVR suffered sufficient histological damage to affect their behaviour.

Effects of UVR on fish that operate at the cellular level are also known (Anderson 1990; Charron et al. 2000; Häkkinen et al. 2003), so it is possible that the reduced levels of aggression that we observed were due to such an effect that produced no overt signs of distress. We think that this is unlikely. If the mechanism were physiological, then we would expect that a recovery period would be required for the physiological changes to reverse and "normal" levels of aggression to reappear. However, all of the behavioural responses to UVR that we observed were proportional to the intensity of PAR at the time of the observation. If there was a physiological effect of UVR affecting behaviour, then it must have been very labile. Furthermore, if UVR was producing a cumulative toxic effect, then we should have been able to detect some time dependency in that effect, i.e., total time of exposure should have been a significant covariate, but there was none.

A third possible mechanism explaining the reduction in agonistic interactions under UVR exposure is that juvenile coho hide from UVR (Kelly and Bothwell 2002) and in doing so increase their degree of visual isolation from neighbours. The colours and body shape of juvenile coho in streams are suited to visually mediated interactions (Dill 1978; Swain and Holtby 1989; Azuma and Iwata 1994), and their full repertoire of agonistic interactions can easily be elicited through mirror-image stimulation (Swain and Holtby 1989; Swain and Riddell 1990; Holtby et al. 1993).

The ability to avoid UVR and to hide from it (Kelly and Bothwell 2002) and the presence in the skin of a photo-induced chemical that absorbs UVR (Fabacher and Little 1996; Bothwell, unpublished data) suggest that coho are well adapted to small shallow streams that may be exposed to UVR. In midsummer, juvenile coho prefer habitat where open and well-lit areas for foraging are interspersed with in-stream cover such as coarse and fine woody debris, waterfalls, and rocks (Giannico 2000). Although juvenile coho are consistently associated with cover of various kinds, they generally are not found within that cover (Bugert and Bjorn 1991; Fausch 1993) and are consequently not visually isolated. Juvenile coho may avoid close association with cover because it interferes with locating prey (Giannico 2000), which might also partially explain why smaller individuals prefer open habitats even in the presence of predators (Reinhardt and Healey 1997; Reinhardt 1999).

Table 3. Summaries of the analysis of covariance (ANCOVA) analyses related to agonistic behaviours.

Model parameter (eq. 1)	μ	$\beta_{\text{within PAR flux}}$	$\beta'_{\text{within SEEN}}$	α_{PAR}	$\alpha_{\text{PAR+UVA}}$	$\alpha_{\text{PAR+UVA+UVB}}$
(*a*) log(1 + approaches per fish SEEN)						
Parameter estimate	0.416	–0.139	0.163	0.339	–0.120	–0.219
Tests of main effects		$F_{[1,40]}$ = 8.50**	$F_{[1,40]}$ = 2.00 NS	$F_{[2,40]}$ = 7.26**		
Post hoc test 1: PAR > (PAR + UVA and PAR + UVA + UVB)	$F_{[1,40]}$ = 14.0***					
Post hoc test 2: PAR + UVA = PAR + UVA + UVB		$F_{[1,40]}$ = 0.38 NS				
(*b*) log(1 + chases per fish SEEN)						
Parameter estimate	0.006	–0.131	0.162	0.165	0.030	–0.195
Tests of main effects		$F_{[1,40]}$ = 8.87**	$F_{[1,40]}$ = 2.35 NS	$F_{[2,40]}$ = 3.24*		
Post hoc test 1: PAR > (PAR + UVA and PAR + UVA + UVB)	$F_{[1,40]}$ = 4.03*					
Post hoc test 2: PAR + UVA = PAR + UVA + UVB		$F_{[1,40]}$ = 2.38 NS				
(*c*) log(1 + nips per fish SEEN)						
Parameter estimate	–0.362	–0.064	0.184	0.213	–0.010	–0.203
Tests of main effects		$F_{[1,40]}$ = 3.42 NS	$F_{[1,40]}$ = 4.88* NS	$F_{[2,40]}$ = 6.76**		
Post hoc test 1: PAR > (PAR + UVA and PAR + UVA + UVB)	$F_{[1,40]}$ = 10.5***					
Post hoc test 2: PAR + UVA = PAR + UVA + UVB		$F_{[1,40]}$ = 2.79 NS				
(*d*) log(1 + (approaches + chases + nips) per fish SEEN)						
Parameter estimate	0.311	–0.202	0.278	0.431	–0.093	–0.338
Tests of main effects		$F_{[1,40]}$ = 10.5**	$F_{[1,40]}$ = 3.44 NS	$F_{[2,40]}$ = 7.48**		
Post hoc test 1: PAR > (PAR + UVA and PAR + UVA + UVB)	$F_{[1,40]}$ = 13.4***					
Post hoc test 2: PAR + UVA = PAR + UVA + UVB		$F_{[1,40]}$ = 1.40 NS				
(*e*) log(1 + total time (s) of agonistic interactions per fish SEEN)						
Parameter estimate	–0.172	–0.278	0.534	0.584	–0.0783	–0.0506
Tests of main effects		$F_{[1,40]}$ = 8.19**	$F_{[1,40]}$ = 3.93*	$F_{[2,40]}$ = 4.52**		
Post hoc test 1: PAR > (PAR + UVA and PAR + UVA + UVB)	$F_{[1,40]}$ = 10.1**					
Post hoc test 2: PAR + UVA = PAR + UVA + UVB		$F_{[1,40]}$ = 1.74 NS				
(*f*) log(1 + time (s) per agonistic interaction)						
Parameter estimate	0.435	–0.0741	0.183	0.022	0.0751	–0.0972
Tests of main effects		$F_{[1,33]}$ = 2.07 NS	$F_{[1,33]}$ = 1.97 NS	$F_{[2,33]}$ = 0.533 NS		
Post hoc test 1: PAR > (PAR + UVA and PAR + UVA + UVB)	$F_{[1,33]}$ = 0.056 NS					
Post hoc test 2: PAR + UVA = PAR + UVA + UVB	$F_{[1,33]}$ = 0.982 NS					

Note: The dependent variables were (*a*) approaches, (*b*) chases, (*c*) nips, (*d*) the sum of (*a*) to (*c*), (*e*) total time (*s*) interacting, and (*f*) time (*s*) per interaction. Variables (*a*) to (*e*) were standardized by the number of fish SEEN, and all variables were log-normalized. The format of the table is described in the caption to Table 1. Probability levels for hypothesis tests are indicated: NS, $P > 0.05$; *, $P \le 0.05$; **, $P \le 0.01$; ***, $P \le 0.001$.

The effects of woody debris on the densities of stream fishes have been extensively documented (Sedell et al. 1984; Fausch and Northcote 1992; Neumann and Wildman 2002), although most of the emphasis has been on the role of debris during the winter (e.g., Murphy and Koski 1989; Hartman and Scrivener 1990; Giannico and Hinch 2003). Localized increases in juvenile salmonid densities have been observed in association with riparian disturbance, canopy removal, and the introduction of small organic debris (e.g., Scrivener and Andersen 1984). Culp et al. (1996) attributed this effect to the addition of structural complexity that afforded more refuges from predators and from which to stage foraging forays. Others have attributed increased densities to increased levels of food due to the trophic effects of increasing light levels (Bilby and Bisson 1992) or to more complex interactions involving temperature, growing season, and size-dependent predation (Holtby 1988).

A more parsimonious explanation for an increase in density is that more fish are present because the small debris that often accompanies streamside disturbance increases visual isolation and allows more fish to occupy the same habitat (Grant and Kramer 1990). Increased summer densities are accompanied with density-dependent decreases in average size at the end of the summer (Holtby 1988), and because overwinter survival is size-dependent (Quinn and Peterson 1996), reductions in overwinter survival and smolt production at least partially offset the benefits of increased stream temperatures following canopy removal (Holtby 1988). Thus, it is possible that through avoidance behaviour, UVR can have a detectable but indirect effect on smolt production. This effect might extend to the marine phase of coho life history as juvenile growth in the summer also partially determines smolt size and smolt size can be directly related to ocean survival (Holtby et al. 1990; Pearcy 1992).

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Depth-integrated, continuous estimates of metabolism in a clear-water lake

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Abstract: High-frequency dissolved oxygen (DO) measurements have been used for estimating gross primary production (GPP) and respiration (*R*) in lake ecosystems. Most researchers have determined GPP and *R* only in surface waters, a practice that may underestimate *R* in general and GPP in clear-water lakes in particular. We deployed oxygen sondes at multiple sites and depths in a clear-water lake. Rates of GPP or *R* were similar horizontally over the surface waters of the lake. Diel DO signals weakened with depth; however, removing noise from the data, by either wavelet transforms or moving averages, enhanced our ability to resolve diel metabolic signals. While GPP declined sharply with depth, *R* was unrelated to depth. The majority of GPP and *R* occurred in the upper mixed layer, but deeper water accounted for 14%–28% of GPP and 20%–43% of *R*, depending on the statistical filtering technique used. GPP and *R* were nearly in balance in the surface waters, but for the entire lake *R* exceeded GPP, and net ecosystem production was negative. Deployment of oxygen sondes in various habitats and at multiple depths allows for a more complete estimate of whole-lake metabolism and a better understanding of the spatial and temporal complexity of lakes.

Résumé : Des mesures d'oxygène dissous (DO) répétées à haute fréquence servent couramment à estimer la production primaire brute (GPP) et la respiration (*R*) dans les écosystèmes lacustres. La plupart des chercheurs mesurent GPP et *R* seulement dans les eaux superficielles, ce qui peut sous-estimer *R* de façon générale et GPP particulièrement dans les lacs à eau claire. Nous avons installé des sondes à oxygène dans plusieurs sites et à diverses profondeurs dans un lac à eau claire. Les taux de GPP et de *R* sont semblables à une même profondeur sur toute l'étendue du lac. Les signaux journaliers de DO s'affaiblissent en profondeur; cependant, le retrait du bruit des données, soit par des transformations en ondelettes ou des moyennes glissantes, nous permet d'interpréter les signaux métaboliques journaliers. Alors que GPP diminue fortement en profondeur, *R* est indépendante de la profondeur. La plus grande partie de GPP et de *R* se produit dans la couche de mélange supérieure, mais les eaux profondes sont responsables de 14–28 % de GPP et de 20–43 % de *R* selon la technique de filtrage statistique retenue. GPP et *R* sont presque en équilibre dans les eaux superficielles, mais dans l'ensemble du lac, *R* est plus importante que GPP et la production nette de l'écosystème est négative. L'installation de sondes d'oxygène dans divers habitats et à plusieurs profondeurs permet ainsi une estimation plus complète du métabolisme du lac entier et une meilleure compréhension de la complexité spatiale et temporelle des lacs.

[Traduit par la Rédaction]

Introduction

In situ sondes fitted with sensitive and accurate oxygen probes have become a useful tool for estimating lake ecosystem metabolism (Cole et al. 2000; Hanson et al. 2003; Lauster et al. 2006). By continuously measuring in situ changes in dissolved oxygen (DO) at high frequency, automated sondes enable the estimate of net ecosystem production (NEP), which is the balance between gross primary production (GPP) and respiration (*R*) (Odum 1956; Lovett et al. 2006).

The sonde method provides an alternative to more traditional methods of measuring metabolism that only use discrete samples. Two approaches have typically been used to estimate lake metabolism: bottle incubations that measure changes of metabolic components in a closed system and free water methods that measure changes of gasses in an open system. Bottle incubations estimate primary production by measuring the change in DO (Carignan et al. 2000) or the uptake of ^{14}C (Peterson 1980; del Giorgio and Peters 1994) that occurs in a contained sample over a specific amount of time and usually under controlled temperature and light conditions. Free water methods estimate GPP and *R* by measuring in situ changes in dissolved gases and include both continuous (sondes) and discrete sampling approaches (Odum 1956; Howarth et al. 1996; Bachmann et al. 2000). Estimates of lake metabolism based on discrete samples (from either incubations or free water approaches) could lead to erroneous conclusions about the trophic status of a lake because important dynamics are missed by limited sam-

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pling (Staehr and Sand-Jensen 2007). Continuous sampling by sondes overcomes many of the limitations of discrete samples and make it possible to measure metabolism in a wide variety of systems (Caraco and Cole 2002; Gelda and Effler 2002; Hanson et al. 2003).

Most previous studies using sondes in lakes have deployed them only at a central station in the upper mixed layer. Estimates from these deployments are representative of surface water metabolism only. Researchers have either avoided trying to measure metabolism in deeper water or assumed that the single sonde samples water that is representative of the entire surface layer and that the majority of lake metabolism occurs in the upper mixed layer (Cole et al. 2000; Hanson et al. 2003). Recently, there has been an increased focus on measuring the relative importance of littoral habitats as contributors to whole-lake processes, including primary production (Lodge et al. 1998; Vadeboncoeur et al. 2001, 2002). Several studies have deployed sondes in various sites in the surface waters and found that littoral metabolism can vary greatly from that of the pelagic, suggesting that metabolism estimates made in pelagic surface waters may miss a large portion of whole-ecosystem metabolism (Caraco and Cole 2002; Lauster et al. 2006; Van de Bogert et al. 2007). While these recent studies moved beyond the tradition of using one central pelagic sonde and explored spatial heterogeneity in surface waters, the observations were, nevertheless, still restricted to the upper mixed layer.

In clear-water lakes, light often penetrates well below the mixed layer, so that there is considerable primary production in deeper water. For a variety of clear-water lakes, the chlorophyll *a* maxima often occur below the mixed layer, extending even to regions of light as low as 1% of surface irradiance (Fee 1976; St. Amand and Carpenter 1993). These deep chlorophyll maxima indicate that there may be substantial primary production below the mixed layer, which would not be sampled by surface water sondes. Primary production has long been measured over depth using the ^{14}C bottle technique, and many earlier studies measured substantial production in deeper water (e.g., Saunders et al. 1962; Megard and Smith 1974; Carpenter et al. 1986). While results from ^{14}C methods indicate there is significant, measurable net primary production in deep waters, prior studies using these techniques could not measure in situ high-frequency variation in production and could not measure *R*, GPP, or NEP as is possible with DO sondes. Automated devices have been developed to profile the water column using DO sondes (Betts 1998; Branco et al. 2005), but few studies have used these devices to estimate lake metabolism at multiple depths. A notable exception was a study that used an automated DO profiler to calculate metabolism at 1 m intervals to depths up to 8 m. However, all of the estimates in this work were made within the mixed layer (Gelda and Effler 2002). Rarely have studies used sondes to explore metabolism below the upper mixed layer.

There are, however, possible problems with using sondes below the mixed layer. Strong temperature and density gradients establish a series of small layers within the metalimnion that have high relative thermal resistance to mixing. Because the water below the mixed layer is not necessarily well mixed (MacIntyre 1993), it may be difficult to determine what portion of the water column is actually represented by the oxygen measured by the sonde. Additionally, the strong oxygen and temperature gradients within the metalimnion have the potential to cause substantial noise in the sonde data if seiches or other processes cause different water masses to move past the probes. This noise could obscure the diel DO signal associated with metabolism, especially if the diel signal weakens with depth as light decreases.

In this study, we use DO sondes to investigate how metabolism changes horizontally within the mixed layer and vertically over depth in a north temperate, clear-water lake. Additionally, we integrate our estimates over depth and across the entire volume of the lake to produce a whole-lake estimate of metabolism and examine the relative contributions of each depth to the entire system. We also employ both moving averages and wavelet transforms to filter our DO time series to reduce non-diel noise and improve resolution of the metabolic signal.

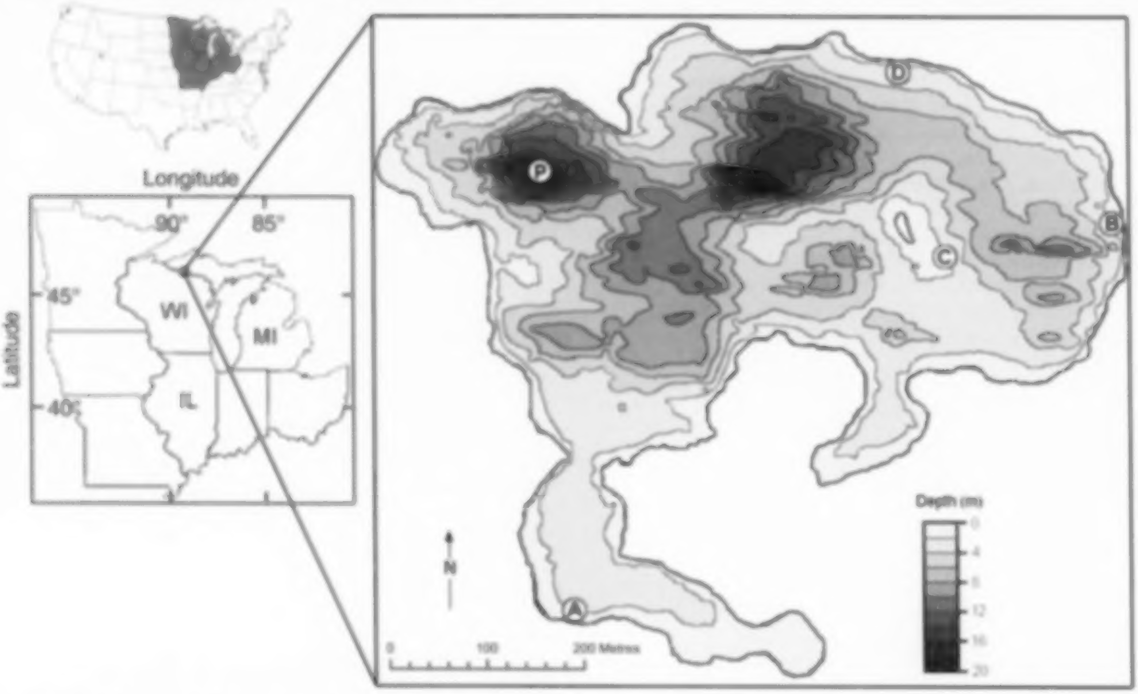
Materials and methods

We sampled Crampton Lake, located at the University of Notre Dame Environmental Research Center in Land O' Lakes, Wisconsin (46°12′N, 89°28′W), from 1 June to 1 September 2005. Crampton is a 25.7 ha, clear-water lake that strongly stratifies during the summer, with an average upper mixed layer depth of ~4 m. The maximum depth is 18.7 m, and the average depth is 5 m.

We deployed sondes at eight sites throughout the lake in both littoral and pelagic waters to measure free water DO and temperature at 5 min intervals for the duration of the study. Four littoral sondes were deployed at a depth of 1 m below the surface where the lake was about 2 m deep (Fig. 1). All littoral sites had similar organic substrates and sparse or no macrophytes. Macrophytes that were present consisted of mainly *Sparganium* spp. and *Eriocaulon aquaticum*. Four other sondes were deployed in the pelagic waters from a buoy moored at the deepest part of the lake. These sondes were deployed at depths of 1, 3, 5, and 8 m. We used YSI 600XLM, 6000UPG, and 6920 sondes fitted with rapid pulse oxygen probes (models 6562, 6030, and 6562, respectively) and temperature probes. All sondes were calibrated in water-saturated air prior to deployment and checked in water-saturated air upon recovery. Each week the sondes were removed for maintenance and recalibration. Calibrations before and after deployments were used to correct for electrode drift, with the assumption that it was linear. We used nine sondes for the eight sites so that we could get continuous measurements at the pelagic 1 m site by using the ninth sonde during the maintenance and calibration period. The placement of sondes was randomized among lake sites to remove any bias from differences in individual sondes.

Profiles of temperature and DO were taken weekly with a YSI model 58 DO meter, and the depth of the mixed layer (Z_{mix}) was determined to occur at the point where temperature changed more than 1 °C per half metre. Weekly light profiles were taken using LI-COR photosynthetically active radiation (PAR) sensors (models LI-190 and LI-193) and an LI-1000 datalogger. A profile of chlorophyll *a* concentration was made each week using a horizontal Van Dorn sampler to

Fig. 1. Crampton Lake bathymetry. Contour lines show depth at 2 m intervals. Letters indicate sonde locations. Littoral sites are denoted by letters A–D, while the pelagic site is denoted by P.



collect water at depths of 100%, 50%, 25%, 10%, 5%, and 1% surface irradiance as calculated from the light profiles. Samples were filtered, frozen, and later analyzed with a fluorometer after methanol extraction (Holm-Hansen and Riemann 1978; Marker et al. 1980). Wind speed at 2 m above the water surface and PAR were sampled every 5 min from a buoy deployed at the pelagic site.

Metabolic calculations are based on those outlined in Cole et al. (2000) and will only be described here briefly. These calculations were made using a program written by the authors in MATLAB (version 7.3, The Mathworks Inc., Natick, Massachusetts). The change in DO over a 5 min interval at any one sensor is assumed to result from three processes: net ecosystem production (NEP = GPP – R), diffusive exchange with the atmosphere (D), and other inputs and outputs of DO (A) such as flux between thermal layers and lateral flows.

$$(1) \qquad \Delta\mathrm{DO} = \mathrm{NEP} + D + A$$

For this calculation, we assumed that each depth layer was a closed system (except for atmospheric exchange in the mixed layer) such that there were no other inputs or outputs of DO (i.e., $A = 0$). Previous studies have indicated that diffusive exchange between depth layers is minimal (Cole and Pace 1998; Gelda and Effler 2002). It is possible that processes, such as internal waves, could alter the DO signal measured by the sondes. We assumed these components of the DO signal, which occur at frequencies much higher than diel, are noise, and we reduced or removed these effects through filtering (see below). The consequences of our assumption are discussed below.

Diffusion with the atmosphere is governed by the departure of the DO concentration in the water from atmospheric equilibrium ($\mathrm{DO}_{\mathrm{sat}}$), and the gas piston velocity for oxygen (k) at a given temperature.

$$(2) \qquad D = k(\mathrm{DO}_{\mathrm{sat}} - \mathrm{DO})$$

D can be either positive (addition of DO to system) or negative (removal of DO from system). We used wind speed measured on the lake to predict k_{600} from the equations of Cole and Caraco (1998) at 5 min intervals. k was calculated from k_{600} using the Schmidt number equations of Jahne et al. (1987). Once atmospheric exchange is calculated, we can estimate NEP at any given time in the surface water. Since the sondes in the metalimnion and hypolimnion were isolated from the atmosphere, we assumed $D = 0$; thus the change in oxygen is equal to NEP for those layers. Because there is no GPP at night, we assume nighttime R equals nighttime NEP. R was measured from 1 h past sunset until 1 h before sunrise. During the day, NEP is a result of the balance between GPP and R. NEP was calculated from sunrise to sunset. We cannot directly measure R during the day, but if we assume that the daytime rate of R is equal to that of nighttime R (Cole et al. 2000; Hanson et al. 2003; Lauster et al. 2006), then we can estimate GPP by adding daytime NEP and R. It is likely that daytime R exceeds nighttime R (Pace and Prairie 2005; Tobias et al. 2007), which would underestimate the magnitudes of GPP and R, but would not have an effect on NEP (Cole et al. 2000). The 5 min estimates of GPP, R, and NEP were accumulated over each 24 h period during the deployment, and these daily values were then averaged over the entire season. For ease of comparison and to emphasize the aspects of oxygen production and consumption during metabolism, we present GPP values as positive and *R* values as negative.

The metabolism estimates from the four pelagic sondes were used to calculate a depth-integrated estimate of whole-lake metabolism. To do this, we defined boundaries to represent the layers of the lake each sonde was measuring. The 1 m sonde was assumed to measure the water from the surface to the depth of the mixed layer (Z_{mix}), as has been done in previous studies of surface water metabolism (Cole et al. 2000; Hanson et al. 2003; Lauster et al. 2006). However, below the mixed layer there are no clear boundaries to define what each sonde measured. We partitioned the remaining water column such that the 3 m sonde measured from Z_{mix} to 4 m, the 5 m sonde measured from 4 to 6.5 m, and the 8 m sonde measured from 6.5 m to the bottom. The consistency in assigning the depth layers was complicated by the deepening of Z_{mix} from 2.5 m at the beginning of the study to 6.5 m at the end. This caused the 3 and 5 m sondes to reside in the mixed layer along with the 1 m sonde for portions of the sampling period. On days when the mixed layer contained more than one sonde, the metabolism values from those sondes were averaged. Therefore, specific results presented below for the 3 and 5 m depth layers only include days when these depths were not part of the mixed layer. Volumetric metabolic rates were calculated daily for each layer and multiplied by the daily volume of that layer as determined from a hypsometric table and the daily value of Z_{mix}. The estimates from each layer were added to give daily values of whole-lake metabolism, which were then averaged over the entire season. The whole-lake values were divided by the lake area to obtain areal rates of metabolism. In this study, "whole-lake" refers to a depth-integrated, volume-corrected estimate of metabolism for the entire lake.

Variations in DO due to advection and other physical factors can obscure the GPP and *R* signals, which vary on a diel basis with light, and cause erroneous interpretations of the results. To clarify the diel components of the pelagic DO data, we used two different approaches to filter all DO time series prior to calculating metabolism. The first approach used a wavelet transform; the second approach used a more basic moving average. Although wavelet transforms have not been frequently used to filter ecological data, this technique is well-established in other fields and is particularly useful for analyzing and filtering noisy signals with intermittent or no periodicities (Addison 2002). We employed a Symlet wavelet transform using MATLAB software (version 7.4) to remove the noise from the DO data. We tested wavelet transforms at 160 and 320 min scales, but chose to remove noise at the 160 min scale based on visual inspection, because it appeared to remove high-frequency variability while preserving most of the diel signal. Although an analysis of specific wavelet and filter scale selection was beyond the scope of this paper, we suggest this as an area of further exploration. Because wavelets are fairly new to ecology, we also used a simple alternative, the moving average, to filter the DO data for comparison. We tested moving averages of 1, 2, and 4 h (i.e., 12, 24, and 48 DO observations). Based on visual inspection, the 2 h moving average removed the most noise while still maintaining a good fit with the test data, so we used this filter on all data. A robust comparison of the two filtering techniques is beyond the scope of this study, but we make limited comparisons below.

Results

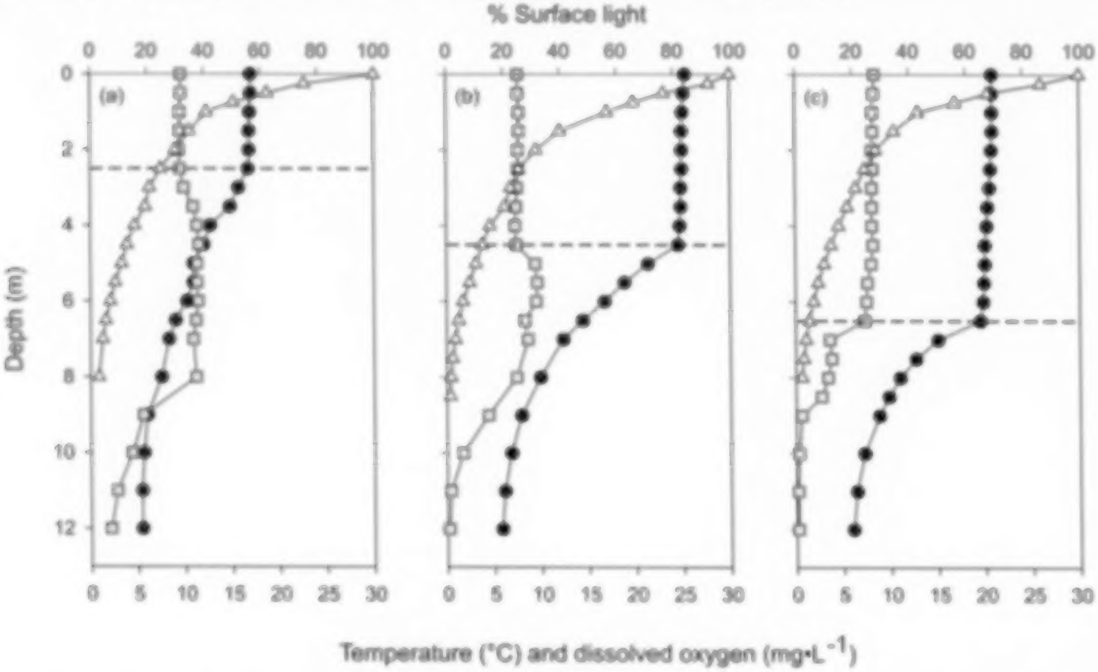
Temperature and DO profiles revealed clear stratification of the water column for the entire study period and a deepening of the mixed layer over the course of the summer (Fig. 2). The DO peak occurred below Z_{mix} for much of the season (60% of deployment days). Light penetration extended well beyond the mixed layer, especially before Z_{mix} began to deepen later in the summer (Fig. 2). Z_{mix} ranged from 2 to 6.5 m and averaged 4 m over the course of the season. On average, 14% of surface irradiance reached Z_{mix}, and 1% of surface irradiance reached 8.9 m. When we averaged the weekly chlorophyll *a* profiles, the average chlorophyll *a* maximum occurred below the mixed layer at 6.3 m (at the 5% light depth) and ranged from 2.6 to 9 m.

DO concentrations and diel patterns were similar across the surface waters, but showed increasing noise with depth. The four littoral sondes and the pelagic 1 m sonde had clear diel DO signals that corresponded with PAR, which is a strong indication of metabolism. However, the diel signal weakened with depth and was obscured by noise (i.e., other factors changed DO) at 8 m (Fig. 3).

Volumetric rates of metabolism were similar across the surface waters of the lake (Fig. 4). While GPP tended to be similar between the littoral sites (A–D) and the pelagic 1 m site (P), *R* was more variable between sites with littoral rates both higher and lower than pelagic rates. Those sites with the highest rates of GPP also had the highest rates of *R*, resulting in rates of NEP that were in balance or slightly negative. The sites with the lowest rates of GPP also had the lowest rates of *R* and positive rates of NEP. To compare these rates among sites, daily values of metabolism from the four littoral sites were each compared with site P using paired *t* tests. Each of the littoral sites had at least one gap in the daily series due to sonde malfunctions (*n* ranged from 50 to 64 days). Because of the gaps, the sites were compared only on days when both had data. There were no significant differences in GPP or NEP between any of the littoral sites and site P (*p* ranged from 0.07 to 0.81). Sites A and D both differed significantly from site P in the rates of *R* (paired *t* tests: $n = 64$, $p = 0.02$; $n = 62$, $p = 0.03$, respectively). The result at site D is surprising because the differences do not appear significant in Fig. 4. This is caused by the gaps in the data, which resulted in an elevated mean rate of *R* at site P for this comparison. Although the significant result at site D may be spurious, we conclude there was some modest spatial heterogeneity in rates of *R* across the surface waters in Crampton Lake.

While surface estimates of GPP were similar over space, the rates of GPP decreased dramatically with depth (Fig. 5). Rates ranged from 12.1 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$ in the mixed layer to 4.2 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$ at 8 m. The mean rate of GPP from the 3 m depth layer was nearly equal to that of the mixed layer. There was no trend with *R* and depth. The highest *R* occurred at 3 m, while the lowest was at 5 m (–18.1 and –10.64 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$, respectively). Estimates of NEP for the entire season varied

Fig. 2. Temperature (solid circles), dissolved oxygen (shaded squares), and light (open triangles) profiles for Crampton Lake on (*a*) 31 May, (*b*) 25 July, and (*c*) 9 September 2007. Broken lines indicate the depth of the mixed layer (Z_{mix}).



across the layers but were always negative and ranged from –0.4 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$ in the mixed layer to –10.8 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$ at 8 m. Although the seasonal estimates of NEP were negative, the daily NEP estimates at 5 m were positive for many days early in the season. Daily rates of metabolism had no strong seasonal trends and were increasingly variable with depth. The standard deviations of the daily rates of GPP at 1 and 3 m were about equal to the mean. At 5 m, the standard deviation was more than twice as large as the mean, and at 8 m the standard deviation was more than 10 times the mean of the daily GPP values.

Of the 91 days of deployment, the mixed layer included the 3 m sonde for 69 days; the 5 m sonde was only in the mixed layer for 17 days. While in the mixed layer, the mean volumetric estimate of GPP from the 3 m sonde was similar to the mean estimate from the 1 m sonde (12.5 and 13.8 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$, respectively), but the estimate from the 5 m sonde was lower (7.8 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$), suggesting that the deeper portions of the apparent upper mixed layer are not as well mixed.

The depth-integrated whole-lake estimate of metabolism (±95% confidence interval) was 51.4 ± 9.9, –66.6 ± 8.9, and –15.2 ± 7.5 mmol $O_2 \cdot m^{-2} \cdot day^{-1}$ for GPP, *R*, and NEP, respectively. The mixed layer comprised a majority of both GPP and *R* (72% and 57%, respectively); however, that meant 28% of GPP and 43% of *R* occurred below the mixed layer (Fig. 6). The contribution of each layer to whole-lake metabolism changed over the course of the season. Early in the season, the depths below the mixed layer contributed an even larger portion. In June, 48% of GPP and 69% of *R* occurred below the mixed layer. These contributions declined over the course of the season, which was mainly the result of the deepening of the mixed layer to include the 3 and 5 m layers.

Our two approaches to filtering the DO time series were able to reduce noise and helped capture the diel signal (Fig. 3). Visual inspection of the filtered data indicated that the wavelet filter was better than the moving average at removing the high level of noise at 8 m while still maintaining the diel signal at 1 m where there was less noise. The two filtering approaches resulted in different estimates of whole-lake metabolism (Fig. 6, Table 1). However, comparisons of the daily estimates from all filters in Table 1 for each individual layer showed no significant differences among the mean GPP, *R*, or NEP values (Table 2). Both filter types reduced the estimates of GPP and *R* primarily by reducing the rates for the 8 m layer. The moving average produced a reasonable estimate of *R*, but it caused the estimate of GPP at 8 m to become substantially negative. This result (negative GPP) is related to the poorer fit and high noise present at the 8 m depth. Since GPP cannot be negative, we assumed for this analysis that it was zero at 8 m. The wavelet filter was better at reducing the noise at 8 m and caused reduced rates of GPP and *R*. The rates of the 3 m layer were also reduced by filtering, especially using the moving average. Both filters resulted in slight increases in mixed layer GPP over the unfiltered estimates, while the rates of *R* remained the same in the mixed layer after wavelet filtering and increased with application of the moving average filter. Interestingly, estimates for the 5 m layer remained mostly unchanged by both filtering approaches. Like the unfiltered data, the filtered data from the moving average resulted in negative NEP.

Fig. 3. Dissolved oxygen (DO) data at (*a*) 1 m, (*b*) 3 m, (*c*) 5 m, and (*d*) 8 m during a time when the mixed layer only contained the 1 m sonde. Gray lines show the raw, unfiltered DO data, and black lines show filtered data using wavelet transforms. (*e*) Photosynthetically active radiation measurements are shown from the central buoy.

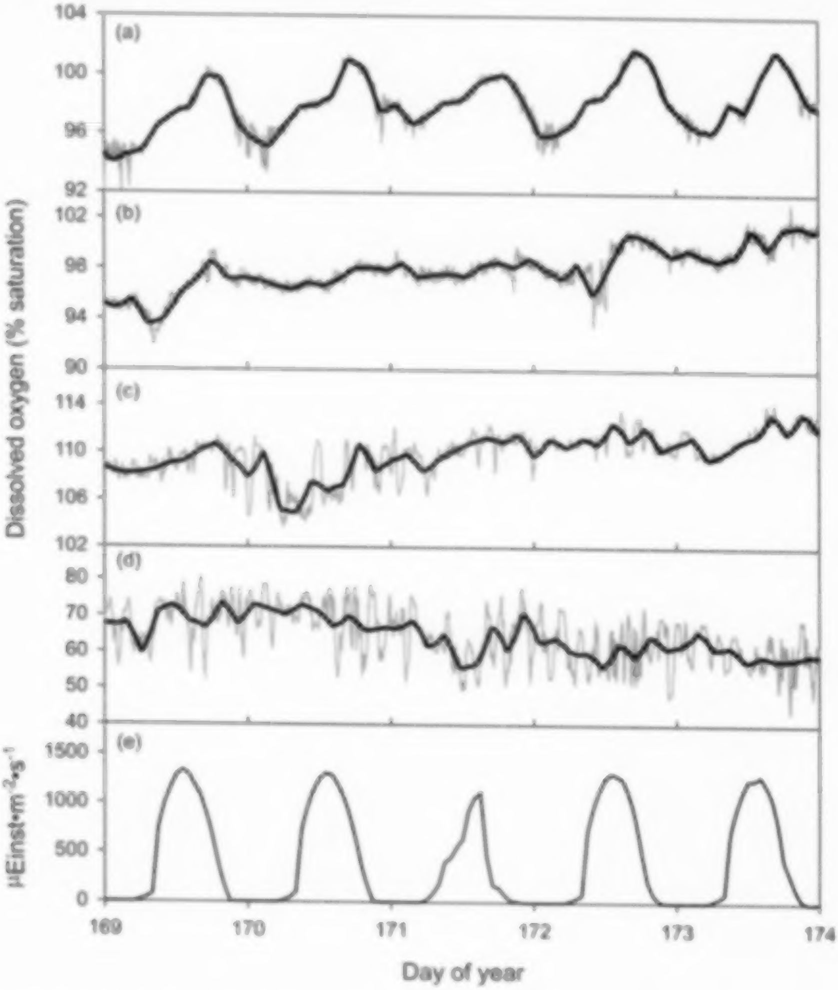


Fig. 4. Mean daily metabolism for the four littoral sites (A–D) and the 1 m pelagic site (P). Results are from the raw, unfiltered data. Error bars show 95% confidence intervals. GPP, gross primary production; *R*, respiration; NEP, net ecosystem production.

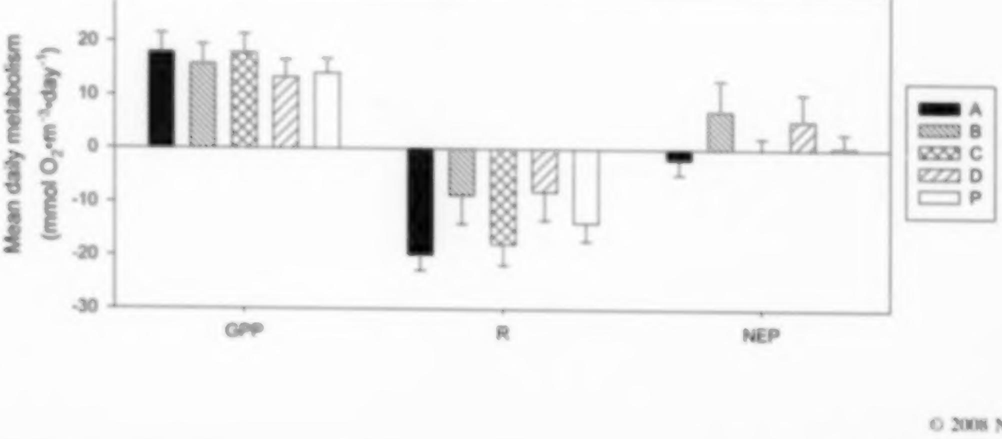


Fig. 5. Mean daily volumetric rates of gross primary production (GPP, open bar), respiration (*R*, solid bar), and net ecosystem production (NEP, crosshatched bar) for each depth layer in the pelagic zone. The mixed layer includes data from the 1, 3, and 5 m sondes whenever they were present in the mixed layer. The 3 and 5 m layers only include data when those sondes were not in the mixed layer. The 8 m layer was always below the mixed layer. Results are from the raw, unfiltered data. Error bars represent standard error.

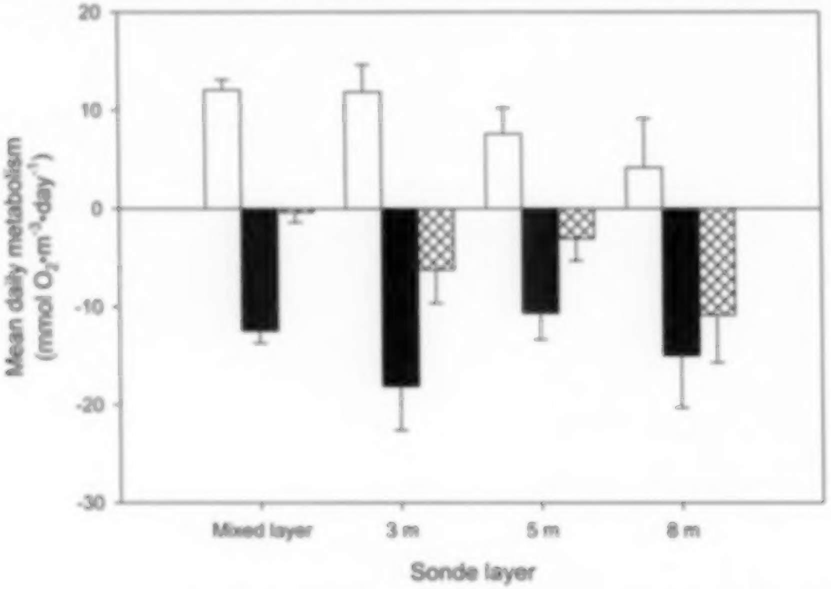


Fig. 6. Depth-integrated whole-lake estimates of metabolism showing contributions from the mixed (solid bars), 3 m (crosshatched bars), 5 m (hatched bars), and 8 m (open bars) layers. The mixed layer includes data from the 1, 3, and 5 m sondes whenever they were present in the mixed layer. The 3 and 5 m layers only include data when those sondes were not in the mixed layer. The 8 m layer was always below the mixed layer. Results are shown from the raw, unfiltered data as well as from data filtered by a wavelet transform (160 min scale) and a moving average (2 h scale). The moving average produced a negative rate of gross primary production (GPP) at 8 m, which we assumed to be zero. Error bars indicate 95% confidence intervals of the total whole-lake estimates. *R*, respiration; NEP, net ecosystem production.

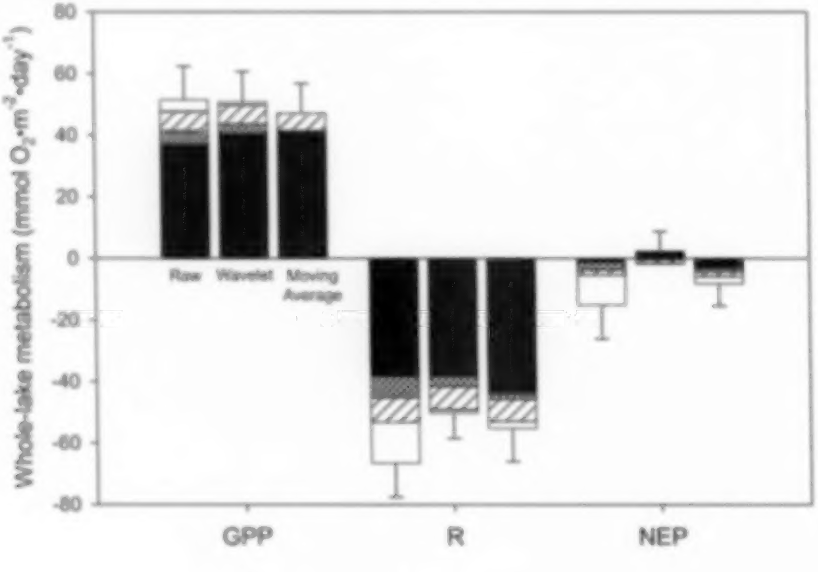


Table 1. Mean daily whole-lake metabolism estimates (mmol $O_2 \cdot m^{-2} \cdot day^{-1}$) from each depth layer using unfiltered data; moving average filtered data at 1, 2, and 4 h timescales; and wavelet-transformed data at 160 and 320 min timescales.

		Moving average			Wavelet transform	
Depth layer	Unfiltered	1 h	2 h	4 h	160 min	320 min
Total						
GPP	51.4 (11.1)	41.2 (9.6)	45.0 (9.9)	41.4 (8.9)	50.7 (10.0)	55.1 (9.4)
R	–66.6 (11.1)	–47.8 (9.8)	–55.0 (11.0)	–52.1 (9.5)	–50.2 (9.1)	–59.1 (7.5)
NEP	–15.2 (11.1)	–6.6 (8.5)	–9.9 (7.4)	–10.7 (6.7)	0.5 (7.7)	–3.9 (7.2)
Mixed layer						
GPP	37.0 (6.0)	37.0 (6.7)	40.7 (6.4)	37.8 (6.7)	40.5 (6.4)	42.6 (6.2)
R	–38.2 (7.1)	–38.5 (7.1)	–43.8 (7.5)	–43.0 (7.6)	–38.2 (6.0)	–42.8 (5.0)
NEP	–1.2 (5.7)	–1.5 (4.6)	–3.1 (4.7)	–5.2 (4.6)	2.3 (4.9)	–0.2 (5.1)
3 m layer						
GPP	4.5 (2.7)	2.6 (2.5)	0.8 (2.3)	1.0 (2.2)	3.1 (2.7)	2.6 (2.0)
R	–7.1 (4.7)	–4.6 (3.3)	–2.1 (2.7)	–2.6 (2.7)	–3.5 (3.4)	–3.9 (2.8)
NEP	–2.6 (2.9)	–2.0 (2.4)	–1.3 (1.6)	–1.6 (1.4)	–0.4 (1.7)	–1.3 (1.7)
5 m layer						
GPP	6.3 (3.8)	6.2 (3.8)	5.6 (4.2)	4.7 (4.1)	6.1 (3.6)	6.5 (4.3)
R	–7.9 (3.8)	–7.8 (2.8)	–7.2 (2.7)	–6.8 (2.6)	–7.3 (2.4)	–8.7 (2.5)
NEP	–1.6 (3.3)	–1.6 (2.7)	–1.6 (2.8)	–2.1 (2.7)	–1.1 (2.7)	–2.2 (3.3)
8 m layer						
GPP	3.7 (8.9)	–4.7 (6.0)	–2.0 (5.6)	–2.1 (5.0)	1.0 (6.7)	3.5 (5.9)
R	–13.5 (9.5)	3.1 (7.6)	–2.0 (6.6)	0.3 (4.9)	–1.2 (5.3)	–3.7 (4.4)
NEP	–9.7 (8.7)	–1.6 (3.1)	–3.9 (4.9)	–1.8 (3.9)	–0.2 (4.8)	–0.2 (4.1)

Note: The total values are from the whole lake and are the sum of each layer. The mixed layer includes data from the 1, 3, and 5 m sondes whenever they were present in the mixed layer. The 3 and 5 m layers only include data when those sondes were not in the mixed layer. The 8 m layer was always below the mixed layer. Values in parentheses are 95% confidence intervals. In all cases, $n = 84$. GPP, gross primary production; *R*, respiration; NEP, net ecosystem production.

while the wavelet filter resulted in a NEP near zero (0.48 mmol $O_2 \cdot m^{-2} \cdot day^{-1}$). As a result of filtering, the portion of GPP and *R* estimated to occur below the mixed layer was respectively reduced from 28% and 43% to 20% and 24% for the wavelet filter and to 14% and 20% for the moving average filter.

Discussion

Rates of metabolism were similar across the surface waters of the lake, although there were some differences in rates of *R* between some of the littoral sites and the single pelagic site. These differences were small and opposing, with sites significantly higher and lower than the pelagic site, and may have averaged out over the entire littoral zone. The effect of any disparity between the littoral and pelagic zones is relatively unimportant at the whole-lake scale because the littoral zone is small in volume relative to the pelagic zone. Therefore, for our analysis, the rates of metabolism from the littoral sites were not included in our whole-lake estimate.

The lack of strong spatial heterogeneity in the surface water metabolism of Crampton Lake deviates from the large differences that both Lauster et al. (2006) and Van de Bogert et al. (2007) found between the pelagic and littoral habitats in other lakes as well as from differences for similar habitats documented by Caraco and Cole (2002) in a large river. Crampton Lake does not have dense, submerged macrophyte beds, and this may be one reason why any differences between littoral and pelagic rates were small. In both the Lauster et al. (2006) and Caraco and Cole (2002) studies, the largest differences were observed in systems or areas with dense macrophyte beds. Mixing caused by wind is another possible reason for the lack of spatial differences in surface water metabolism. Van de Bogert et al. (2007) found that wind acts as a homogenizing force, such that pelagic and littoral signals are indistinguishable on days when the average wind speed at 2 m (above the lake surface) exceeds a threshold of 2.75 $m \cdot s^{-1}$ for an hour. The wind on Crampton Lake reached this threshold on 70% of the days during our study. Site A was the most sheltered from the wind, as wind was predominantly from the southwest, and rates of metabolism at this site were the most different from the pelagic site.

Sondes reliably captured the diel changes in oxygen below the mixed layer at 3 and 5 m. The diel signals at these depths were weaker than those in the mixed layer, but they were still resolvable by our metabolism model, as it produced reasonable estimates of GPP and *R*. In addition, filtering the data enhanced our ability to resolve metabolic (i.e., diel) signals by removing the non-diel (i.e., nonbiological) variability in the DO signal. DO data from the 8 m sonde was not as clear, as high levels of noise made it difficult for our model to resolve the metabolic signal. The moving average filter was unable to reduce the noise at 8 m and recover reasonable metabolic estimates, as GPP tended to be negative using this approach. The wavelet transform was able to reduce the non-diel noise, and this transformation resulted in greatly decreased rates of metabolism at 8 m. This result

Table 2. Results of analysis of variance (ANOVA) tests comparing daily estimates over 84 days of gross primary production (GPP), respiration (*R*), and net ecosystem production (NEP) from the moving average (1, 2, and 4 h) and the wavelet transform (160 and 320 min) filters.

Depth layer	Source	SS	*df*	MS	*F*	*p*
Total						
GPP	Filter	11 712	4	2928	1.49	0.20
	Error	816 266	415	1967		
R	Filter	6 320	4	1580	0.83	0.51
	Error	791 674	415	1908		
NEP	Filter	7 583	4	1896	1.57	0.18
	Error	502 214	415	1210		
Mixed layer						
GPP	Filter	1 658	4	414	0.46	0.77
	Error	376 646	415	908		
R	Filter	2 638	4	659	0.68	0.61
	Error	402 485	415	970		
NEP	Filter	2 888	4	722	1.48	0.21
	Error	202 202	415	487		
3 m layer						
GPP	Filter	386	4	96	0.80	0.53
	Error	50 136	415	121		
R	Filter	350	4	87	0.46	0.77
	Error	79 485	415	192		
NEP	Filter	113	4	28	0.41	0.80
	Error	28 691	415	69		
5 m layer						
GPP	Filter	150	4	38	0.11	0.98
	Error	143 389	415	346		
R	Filter	166	4	42	0.29	0.89
	Error	60 076	415	145		
NEP	Filter	64	4	16	0.09	0.99
	Error	73 802	415	178		
8 m layer						
GPP	Filter	3 054	4	764	1.04	0.39
	Error	306 113	415	738		
R	Filter	2 017	4	504	0.68	0.61
	Error	308 311	415	743		
NEP	Filter	834	4	208	0.42	0.80
	Error	207 885	415	501		

Note: The total values are from the whole lake and are the sum of each layer. The mixed layer includes data from 1, 3, and 5 m sondes whenever they were present in the mixed layer. The 3 and 5 m layers only include data when those sondes were not in the mixed layer. The 8 m layer was always below the mixed layer.

suggests that much of the changes in DO at 8 m were primarily caused by physical rather than biological processes and for the most part did not reflect metabolism.

A complete mass balance of oxygen for any given layer is described in eq. 1, where *A* is the exchange, production, or consumption of oxygen by other physical–chemical processes. In our analyses, we have assumed *A* to be negligible compared with other terms in the equation. To test this assumption, we can estimate the vertical flux of DO between layers that may occur because of large concentration gradients. A large oxygen gradient occurs in Crampton Lake below the oxygen maximum, which is typically at 5 m. The difference in DO between sonde locations at 5 and 8 m during midsummer is approximately 2 $mg \cdot L^{-1}$. Assuming a coefficient of vertical diffusion (K_v) of 0.02 $cm^2 \cdot s^{-1}$, we can estimate the cross-gradient flux of oxygen using standard equations (Jassby and Powell 1975). The flux was 3.6 mmol $O_2 \cdot m^{-2} \cdot day^{-1}$, which was quite small relative to the average whole-lake GPP and *R* estimates of 51.4 and −66.6 mmol $O_2 \cdot m^{-2} \cdot day^{-1}$, respectively. While there are mechanisms of oxygen consumption and production associated with *A*, these appear to be small fluxes relative to metabolic rates. An exception might be for deeper layers, such as the 8 m layer, where metabolic rates are lower so that these fluxes may have a larger impact, especially during episodic mixing events (Ostrovsky et al. 1996). These mixing phenomena may contribute to the considerable noise observed in the 8 m DO data. While inclusion of these fluxes into our oxygen budget may have some effect on our estimates of metabolism for each layer, our estimate of whole-lake metabolism, which includes all layers, may not be affected, since any oxygen lost by a layer through vertical exchange is gained by another layer. If there was a flux of oxygen from 5 to 8 m, then we would have overestimated metabolism in the 5 m layer, but we would also have underestimated metabolism in the 8 m layer by the same amount. Thus, the whole-lake estimate of metabolism would remain the same.

Because both GPP and *R* vary strongly with depth, estimates based on the surface water alone will underestimate whole-lake metabolism. This result is well known from early discrete sampling studies of primary production (Fee 1980), but it is useful to evaluate the degree of underestimation using the sonde approach where daily values of GPP, *R*, and NEP are generated. For example, had we only used the pelagic 1 m sonde in this study, we would have overestimated seasonal rates of GPP and *R* in the upper mixed layer by 13% and 3%, respectively, and underestimated whole-lake GPP by 18% and *R* by 41%.

Our study revealed that rates of metabolism were not constant throughout the apparent upper mixed layer, but were lower in the deeper portions. Our assessment of the depth of the mixed layer is based only on weekly temperature profiles and is too course to capture shorter-term dynamics in changes in the mixing regime that others have observed at a number of time scales (MacIntyre et al. 1999). While we do have high-frequency temperature data from each of the sondes, the data does not have enough vertical resolution to assess these short-term dynamics in thermal structure. The fact that the 5 m sonde on days we assessed it to be in the mixed layer gave different results than those at 1 and 3 m is probably indicative of this dynamic variation in mixing.

At the deepest site (8 m), DO did not vary on an obvious diel cycle with or without statistical filtering. It is possible that the estimates of GPP and *R* for this depth layer were spurious, and variations in DO were caused by either water movements or other processes. Additionally, we overestimated the contribution of the 8 m layer to whole-lake GPP because we extrapolated the 8 m results to the bottom of the lake, even though GPP is probably zero below 10 m. This error, however, is small (~2% of the unfiltered, total whole-lake GPP estimate) because the rate of GPP at 8 m is small, and the volume of water at 10 m and below is only about 5% of the lake volume. Nevertheless, even if we were to disregard GPP and *R* from the 8 m layer, the 1 m sonde alone would still have underestimated whole-lake GPP (through the 5 m depth) by 12% and *R* by 26%. Furthermore, we would have falsely concluded that NEP for the mixed layer (and thus the whole lake) was positive if we had only used the pelagic 1 m sonde. Because *R* was not trended with depth and GPP decreased with depth, it is likely that NEP estimates would be lower in many lakes if depth-integrated values were used.

A single surface sonde is unable to accurately measure metabolism of the whole lake or even of the apparent mixed layer. Using multiple sondes deployed both horizontally and vertically within a lake is essential to accurately estimating whole-lake metabolism. Exactly how many sondes are required for robust estimates is unknown and likely depends on the heterogeneity of the system being studied. The results of this study suggest that thermal partitioning of the water column relates to the biological activity, as expressed in rates of metabolism. Even though past studies have assumed the epilimnion to be well mixed, our DO data from sondes placed near the top and bottom of the epilimnion yield different metabolism estimates, suggesting a certain degree of partitioning within the epilimnion, as has been found elsewhere (Eckert et al. 2002). Although the influence of short-term dynamics in thermal structure on the metabolic rates in the water column is beyond the scope of this study, further investigation of that relationship may prove fruitful.

Ecosystem-level processes are complex and difficult to estimate. The use of automated sensors is greatly enhancing our ability to estimate rates over broader time and space scales. These instruments allow researchers to collect considerably more data at scales that would be impossible using traditional techniques. Sensors are able to continuously sample at intervals of minutes rather than of days or weeks with traditional methods. Simultaneous high-frequency measurements from multiple sensors deployed in various locations allowed us to gauge the relative importance of different habitats and depth layers to whole-lake metabolism. With these advances in observation technology come challenges in signal processing and ecosystem modeling, especially as we begin scaling up estimates from multiple sensors to the whole ecosystem. High-frequency measurements allow for more temporally dense metabolism estimates, but also yield patterns at multiple time scales that can confound our ability to separate the desired signal from noise. Wavelet transforms are one type of filtering that shows promise for separating signals by scale. Furthermore, a tighter coupling between physical and biological processes in our models will help us better understand the relationships among thermal stratification, metabolism, and gas flux. As these techniques are applied to the diversity of aquatic ecosystems, we are sure to appreciate more fully the spatial and temporal complexity of lakes.

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Large-scale responses of nematode communities to chronic otter-trawl disturbance

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Abstract: Nematodes, because of their small size and short life cycles, are thought to be less affected by direct trawling mortality compared with the larger macrofauna. However, nematodes may still be indirectly affected by the physical disturbance of trawling through changing sediment characteristics and food web structure. We determined whether nematode communities on two muddy fishing grounds located in the North Sea and Irish Sea were affected by chronic otter-trawl disturbance and quantified these effects. Nematode abundance, production, and genus richness declined in response to trawling within both areas. Nematode biomass did not respond to trawling intensity. Genus composition was affected by trawling only in the North Sea. The responses in abundance of individual nematode genera to increasing trawling intensity were negative as well as positive. These results indicate that despite their size and fast life cycle, nematodes are affected by intensive trawling on muddy fishing grounds. The loss in secondary production from nematodes can have far-reaching consequences for the integrity of the benthic food web. As bottom trawl fisheries are expanding into ever deeper muddy habitats, the results presented here are an important step towards understanding the global ecosystem effects of bottom trawling.

Résumé : On croit que les nématodes, à cause de leur petite taille et de leur cycle biologique court, subissent moins de mortalité directe due au chalutage que la macrofaune de plus grande taille. Cependant, les nématodes peuvent néanmoins être affectés indirectement par les perturbations physiques causées par le chalutage par la modification des caractéristiques des sédiments et de la structure du réseau alimentaire. Nous déterminons si les peuplements de nématodes sur deux aires de pêche à fond boueux dans la mer du Nord et la mer d'Irlande sont affectés par la perturbation chronique due à l'utilisation de chaluts à panneaux et nous en mesurons les effets. L'abondance, la production et la richesse générique des nématodes diminuent en réaction au chalutage dans les deux régions. La biomasse des nématodes ne change cependant pas en fonction de l'intensité du chalutage. La composition générique n'est affectée par la chatulage que dans la mer du Nord. Les variations des abondances individuelles des différents genres de nématodes en réaction à une augmentation de l'intensité du chalutage peuvent être négatives ou positives. Nos résultats indiquent donc que, malgré leur petite taille et leur cycle biologique court, les nématodes sont perturbés par le chalutage intensif sur les aires de pêche à fond boueux. La perte de production secondaire provenant des nématodes peut avoir des conséquences de longue portée sur l'intégrité du réseau alimentaire benthique. Puisque la pêche au chalut pénètre de plus en plus dans les habitats boueux plus profonds, les résultats de notre étude constituent une étape importante dans la compréhension des effets du chalutage de fond sur l'écosystème global.

[Traduit par la Rédaction]

Introduction

Towed bottom fishing gears, such as beam trawls and otter trawls, are regarded as one of the greatest and most widespread sources of anthropogenic physical disturbance to soft sediments in shelf seas (Jennings and Kaiser 1998; Bergman and van Santbrink 2000; Kaiser et al. 2006). Research over the past two decades has demonstrated that these fishing activities can have far-reaching negative effects on the biodiversity, biomass, and production of benthic communities (Jennings and Kaiser 1998). The majority of studies thus far have focussed primarily on the impacts of trawling on larger benthic macrofauna, because they are thought intrinsically vulnerable to trawl disturbance and because they are relatively easy to sample and identify. In contrast, meiofauna are considered less vulnerable to the direct physical impacts of trawling because of their size and higher intrinsic rates of productivity (Duplisea et al. 2002). Nevertheless, these smaller organisms may be affected indirectly by the physical disturbance of trawl gear through habitat disruption and changes in the macrofauna composition, abundance, and biomass. Previous studies have shown that bottom trawling can modify sediment sorting, grain size, and organic matter profiles; increase silt content; and cause loss of surficial sediment through resuspension and the winnowing of fines (Palanques et al. 2001; Brown et al. 2005; Trimmer et al.

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2005). This physical disruption of the sediments has been demonstrated to ultimately result in a loss of habitat quality for benthic organisms (Watling et al. 2001).

In marine sediments, nematodes are usually numerically dominant and account for 60%–95% of the total meiofauna (Coull 1999). The entire life cycle of many meiofauna can be completed in a matter of weeks (Gee and Warwick 1984), resulting in a much higher production to biomass ratio of meiofauna compared with macrofauna. Thus, despite their negligible biomass, meiofauna can make an important contribution to overall benthic productivity (Alongi and Robertson 1995; Schwinghamer et al. 1998). Meiofauna feed upon bacteria, detritus, diatoms, and algal mats and represent an important source of food for higher trophic levels, such as macrofauna and fish (Coull 1999). In addition, meiofauna have been shown to indirectly affect the microbiota by stimulating bacterial growth and consequently enhance rates of mineralization and nutrient regeneration (Heip et al. 1985). While nematodes are an important ecosystem component in all habitats, they are probably more active in sediments with high amounts of organic matter, such as muddy sediments (Coull 1999).

Little research has been conducted on the response of meiofaunal communities to fishing (Engel and Kvitek 1998; Pranovi et al. 2000; Schratzberger and Jennings 2002) despite their ecologically important role to marine food webs (Gerlach 1971, 1978). For ecosystem-based approaches to fisheries management (Link 2002), the effects of fishing on meiofauna need consideration.

To understand the effects of trawling disturbance at the scale of the fishery, it is necessary to study areas subjected to real fisheries where disturbance occurs on large scales over long time periods. Within the present study, we investigated if nematode communities were affected by chronic otter-trawl disturbance and quantified the response of nematode abundance, biomass, production, and genus composition to chronic otter-trawling. The effects of otter-trawling were investigated at a scale relevant to fishery management with a much higher level of replication than earlier comparative studies, which has been made possible by the advent of high resolution over-flight and satellite monitoring of fishing vessels. We compared the impact of otter trawling on two muddy fishing grounds in the North Sea (Fladen Ground) and the Irish Sea (off the Cumbrian coast) separated by approximately 800 km. Such regional comparisons are useful because they highlight the generality of responses to similar agents of disturbance at a regional scale.

Materials and methods

Study areas

The long-term effects of chronic trawling on benthic meiofauna was investigated in two fishing grounds located in the North Sea (Fladen Ground, Fig. 1*b*) and Irish Sea (off the Cumbrian coast, Fig. 1*c*). The main bottom trawling activity that occurs on both fishing grounds is otter-trawling for gadoid fish and Norway lobster (*Nephrops norvegicus*). In addition, shrimps of the genus *Pandalus* are targeted on the Fladen Ground. The fisheries in both areas operate mainly in spring and early summer. The offshore fishery of the Fladen Ground generally consists of fishing vessels of over 24 m in length that operate for more than a day at a time. In the Irish Sea, because of the proximity to the coast, vessels tend to be day boats under 20 m in length. Both areas are characterized by mild hydrodynamic conditions and consequently comprise muddy sediment deposits with a high silt and clay content (>50%). The areas were selected for investigation because they were of a similar habitat type and had a strong spatial gradient in trawling intensities (Table 1).

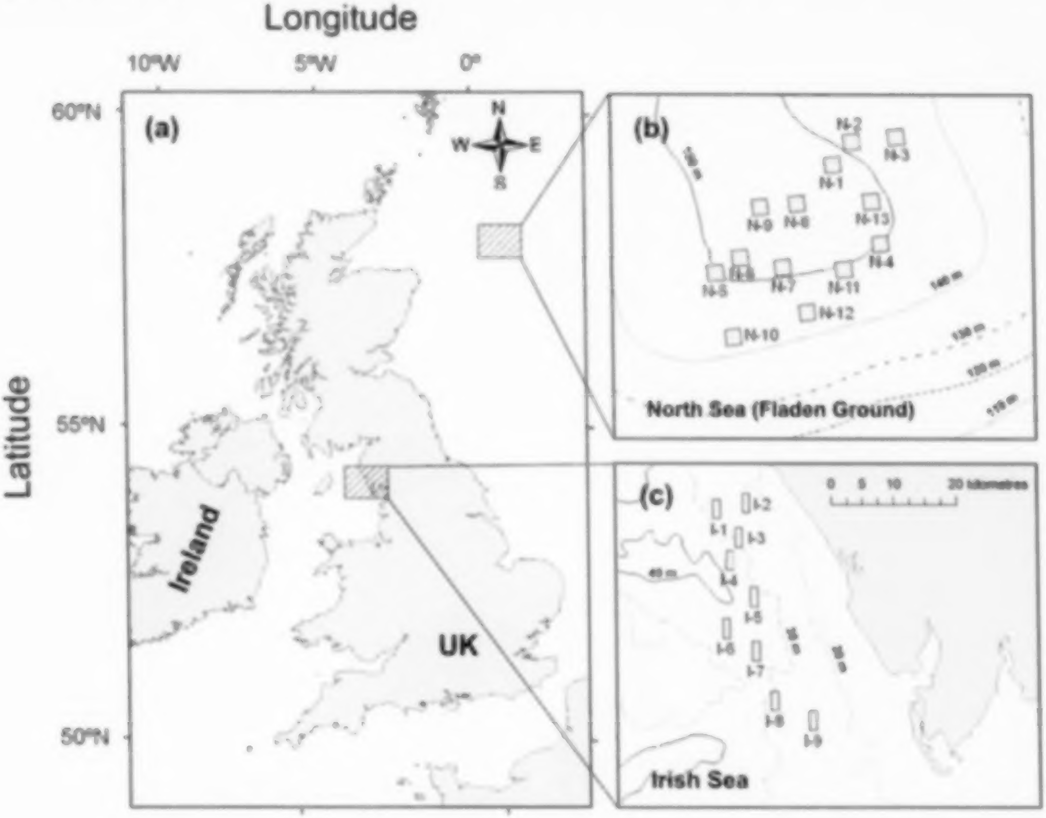
Estimation of fishing effort

The estimation of trawling intensities over the two respective fishing grounds was based on different data sources and therefore required different methodologies. In the North Sea, satellite data from the European Community Vessel Monitoring System (VMS) was used to calculate fishing effort. Vessels over 24 m are required to report their location via satellite at 2 h intervals. Only vessels that undertake fishing trips under 24 h or that exclusively fish within 12 nautical miles (1 nautical mile = 1.852 km) of the shoreline are exempted (Dann et al. 2002). The operational status of vessels (e.g., fishing, steaming, or stationary) was identified from two consecutive positions. Vessels travelling at a speed over 8 knots (1 knot = 1.852 km·h^{-1}) were considered to be steaming and were excluded from the analysis. Similarly, stationary vessels were eliminated as they were assumed not to be fishing. The spatial distribution of fishing vessels was processed within a GIS, and fishing frequency was calculated on a scale of 9 km^2 cells over the extent of the fishing ground. For calculations of trawling intensities, as times trawled per year, an average trawling speed of 2.5 knots and an average gear width of 60 m for otter trawls was used. Trawling intensities on the Fladen Ground were calculated for the period from July 2000 to December 2003. Sampling of the nematode communities on the Fladen Ground was carried out in June 2004.

Owing to the exemption of certain fishing vessels to the reporting process of positional information (see above), VMS data were not available for the fleet operating in the Irish Sea. Almost the entire area of the fishing ground is located within the 12 nautical mile limit, and fishing vessels are below the minimum size for which VMS is mandatory. To estimate fishing effort, over-flight data and logbook records of hours spent fishing per ICES rectangle collected by the UK's Sea Fisheries Inspectorate were used. Spotter planes regularly survey the UK's Exclusive Economic Zone to monitor UK and foreign fishing vessels. Flights over the Irish Sea occur on a weekly basis and record the geographical position, gear type, and activity of fishing vessels indiscriminate of vessel size. From these data, the spatial distribution of active fishing vessels fishing with relevant bottom gears was established for a 5-year period from October 2000 to October 2004. Sampling of the nematode communities off the Cumbrian coast was carried out in November 2004.

As the spatial resolution of this data largely depends on the number of flights conducted, data density is much lower compared with the virtually continuous reported VMS data. Hence, for detailed spatial coverage, it was required to monitor the fishing fleet for a longer period in the Irish Sea. Density of vessels was calculated for 1 km^2 grid cells, with a search radius of 3 km (see Mitchell 1999 for details on density calculations). For the estimation of fishing frequency as

Fig. 1. (*a*) Maps showing the locations of the two areas and the spatial distribution of sampling sites in (*b*) the North Sea (Fladen Ground) and (*c*) the Irish Sea.



times trawled·year^{-1}, the spatial data were combined with data from logbook entries. UK fishermen are by law required to report by gear type and how many hours they spent fishing within ICES rectangles. Thus, the total time reported bottom trawling over the fishing ground (ICES rectangle 37 E6) for the relevant period was divided proportionally to the vessel density information in the 1 km^2 cells. This calculation resulted in cell values of hours fished, which were converted to times trawled·year^{-1} assuming a trawling speed of 2.5 knots and a gear width of 60 m.

Sampling design

Thirteen stations were chosen in the North Sea to cover the maximum possible range of fishing intensities (Fig. 1, Table 1). Each station was designated as a box of 2.5 km × 2.5 km. Five haphazardly distributed 0.1 m^2 Day grabs were taken within each box to sample nematode communities. From each grab, a sample was taken for analysis with a cut-off syringe (1.58 cm^2, approximately 3 cm deep; De Wilde et al. 1986). The samples from the five Day grabs were pooled before analysis to integrate spatial variation in nematode distribution and preserved in 4% buffered formalin solution. Additionally, from all five grabs a sediment sample with a cut-off syringe (1.58 cm^2, ≈6 cm deep) was taken and pooled for spatial integration. Nine sampling stations, 1 km × 2 km boxes, were selected in the Irish Sea to cover the maximum possible range of fishing intensities (Fig. 1, Table 1). At three haphazardly chosen locations within each box, three 0.1 m^2 Day grabs were taken. Using a syringe corer (1.58 cm^2, ≈3 cm deep), three cores were taken at random points within each grab and pooled to integrate spatial variation of meiofaunal distribution on a centimetre scale and preserved in 4% buffered formalin solution for pending laboratory analyses. A single sediment sample was taken from each sampling site within sampling boxes using a cut-off syringe (1.58 cm^2, ≈6 cm deep).

Nematode sample processing and biomass and production estimates

For both areas, the same protocol was followed for sample processing and biomass and production estimates. Meiofauna were extracted from the samples using the method described by Somerfield and Warwick (1996). Nematodes were the dominant meiofaunal taxon (80%–95%) in the samples. Owing to the large number of replicate samples within this study, we identified only 40 randomly selected nematodes to genus level per sample to estimate genus richness for each box (Platt and Warwick 1998*a*, 1998*b*; Warwick et al. 1998). As the main focus of this study was on the broad-scale response of nematode communities to trawling disturbance, a

Table 1. Characteristics of study areas.

Station ID	Station area (km × km)	No. of samples	Trawling frequency (year^{-1})	Depth (m)	Sediment content (%)			Bed shear stress (N·m^{-2})
					Silt	Organic	Water	
North Sea								
N-1	2.5 × 2.5	5	1.59	151	95	6	48	0.08
N-2	2.5 × 2.5	5	3.81	151	96	7	47	0.08
N-3	2.5 × 2.5	5	1.74	150	95	7	47	0.08
N-4	2.5 × 2.5	5	1.17	150	93	7	47	0.08
N-5	2.5 × 2.5	5	0.45	145	93	6	41	0.10
N-6	2.5 × 2.5	5	0.21	146	95	6	44	0.09
N-7	2.5 × 2.5	5	0.79	151	95	6	44	0.09
N-8	2.5 × 2.5	5	1.74	150	95	7	45	0.08
N-9	2.5 × 2.5	5	1.52	148	95	7	48	0.08
N-10	2.5 × 2.5	5	0.26	143	94	5	40	0.11
N-11	2.5 × 2.5	5	1.09	150	95	6	45	0.09
N-12	2.5 × 2.5	5	0.86	150	93	6	43	0.09
N-13	2.5 × 2.5	5	1.80	153	97	7	47	0.08
Irish Sea								
I-1	1 × 2	3	7.52	31	56	5	39	0.22
I-2	1 × 2	3	7.35	26	54	5	40	0.24
I-3	1 × 2	3	10.16	29	70	6	42	0.21
I-4	1 × 2	3	11.81	36	86	6	44	0.21
I-5	1 × 2	3	17.09	31	82	7	42	0.19
I-6	1 × 2	3	10.34	36	61	5	38	0.19
I-7	1 × 2	3	12.06	34	71	7	40	0.17
I-8	1 × 2	3	1.85	28	74	6	46	0.18
I-9	1 × 2	3	1.66	24	77	6	41	0.23

high number of replicates over a large spatial scale was deemed more important than high taxonomic precision. Furthermore, 40 nematodes in each sample were randomly selected for the calculation of biomass (wet mass, WM) and measured under a microscope using an eyepiece graticule, according to Andrassy (1956): wet weight = (length × width^2) × 1 600 000^{-1}, where WM is in micrograms and length and width are in micrometres. If the nematodes had a long, filiform tail, the tail was not included in the measurement. Nematode production was estimated using the following equations (Vranken et al. 1986):

$$\log T_{\min} = 2.202 - 0.0461t + 0.627 \log W$$

$$\text{production:biomass ratio} = 1/T_{\min}\,3D$$

where $T_{\min}$ is the duration of egg to hatch development (days), t is bottom temperature, W is body weight (µg WM), and D is number of days in a year. The average yearly bottom temperature was 7.3 °C on the Fladen Ground and 10 °C on the fishing ground of the Cumbrian coast (ICES Oceanographic Database and Services: www.ices.dk/ocean/dotnet/HydChem/HydChem.aspx; North Sea data 1980–1986 and Irish Sea data 1986–2004). Nematode WM was converted to ash-free dry mass (AFDM) using the conversion factor 1g WM = 0.2 g AFDM (Heip et al. 1985). Although the $T_{\min}$ estimate is based on adult female body weight (Vranken et al. 1986), we used the equations to calculate production for individual nematodes regardless of sex and maturity stage. Nematodes mature early and as there are only small differences between male and female body weight, this seems unlikely to have caused substantial bias in our production estimates.

Sediment samples and bed shear stress

The fraction of particles <63 µm (i.e., mud (silt and clay)) was determined by weight loss following wet-sieving, while coarser fractions were determined by mechanical dry-sieving through stacked Wentworth grade sieves (Holme and McIntyre 1984). Prior to sieving sediment, percent water content of sediment samples was estimated via weight loss after drying to a constant weight at 70 °C. Organic matter content was estimated by weight loss of ≈5 g of dried sediments on ignition at 550 °C for 6 h (Holme and McIntyre 1984).

Bed shear stress was calculated from a two-dimensional hydrodynamic model of the northwest European shelf. For more detailed information on the methodology used, see Hiddink et al. (2006).

Statistical analysis

To investigate the relationship between trawling frequency (year^{-1}) and environmental parameters measured at stations (depth, silt–clay content, organic content, water content, and shear stress), a Pearson correlation analysis was performed for each area. Prior to analysis, all variables were $\log_{10}(n + 1)$-transformed so that the data approximated normality.

The relationship of trawling frequency (year^{-1}) and nematode abundance (m^{-2}), biomass (g WM·m^{-2}), production (g AFDM·m^{-2}·year^{-1}), and genus richness was investigated on the combined data from North Sea and Irish Sea using a

Table 2. Pearson's correlation coefficients (*r*) and *p* values (in parentheses) of the correlations between sediment parameters and trawling frequency for the North Sea and Irish Sea study areas.

Parameter	Silt and clay content (%)	Organic content (%)	Water content (%)	Shear stress ($N \cdot m^{-2}$)	Trawling frequency ($year^{-1}$)
North Sea					
Depth	0.51 (0.079)	0.64 (0.019)*	0.74 (0.004)*	–0.81 (0.001)*	0.73 (0.005)*
Silt and clay content		0.38 (0.204)	0.53 (0.065)	–0.47 (0.110)	0.55 (0.053)
Organic content			0.78 (0.002)*	–0.88 (0.000)*	0.75 (0.003)*
Water content				–0.95 (0.000)*	0.76 (0.003)*
Shear stress					–0.78 (0.002)*
Irish Sea					
Depth	0.16 (0.685)	0.01 (0.969)	–0.08 (0.823)	–0.58 (0.104)	0.64 (0.061)
Silt and clay content		0.83 (0.005)*	0.73 (0.025)*	–0.36 (0.348)	0.16 (0.680)
Organic content			0.56 (0.115)	–0.34 (0.375)	0.43 (0.248)
Water content				–0.27 (0.485)	–0.09 (0.819)
Shear stress					–0.32 (0.394)

*Significant at $p = 0.05$.

generalized linear model. Univariate community descriptors were assigned as dependant variables, while trawling frequency and location (North Sea, Irish Sea) were assigned as independent variables in the analysis. Both main effects and interaction terms were analysed. Prior to analysis, all variables were $\log_{10}(n + 1)$-transformed.

The response in abundance of individual nematode taxa to trawling intensities was investigated using least square regression analysis. The analysis was performed on $\log_{10}(n + 1)$-transformed abundance ($n \cdot m^{-2}$) and trawling frequency ($year^{-1}$) data. The number of genera responding in the same way in both the North Sea and Irish Sea was analysed by the Fisher exact test to establish if the number of taxa showing a similar response was significantly greater than would have been expected by chance ($p = 0.05$).

To examine the effect of trawling on community composition within the two areas, we used nonparametric multidimensional scaling (MDS) on nematode abundance data (Primer version 6). The analyses were performed on square-root transformed Bray–Curtis percent similarity matrices (Clarke and Warwick 1994). The resulting MDS plots were overlaid with bubble plots of trawling intensity to visualize possible patterns in the community ordinations. Furthermore, the data was tested for seriation to detect any directional trends in community pattern related to trawling intensity (Primer version 6 RELATE routine). The BIOENV routine was used to test which individual or combination of environmental parameters had the strongest relationship with the ordination of nematode abundance data in both areas. (Primer version 6 BIOENV routine).

Results

Trawling frequency and environmental parameters

In the Fladen Ground, trawling frequency was correlated to all but one of the measured environmental variables. Depth, organic content, and water content of the sediment were positively correlated to trawling frequency, while seabed shear stress was negatively correlated to trawling frequency (Table 2). There was no significant relationship between trawling frequency and the silt–clay content of the sediment (Table 2). In the Irish Sea, no significant correlation between trawling frequency and sediment variables existed (Table 2).

Nematode communities

In the North Sea and Irish Sea, 31 and 27 genera of nematodes were identified, respectively. The numerically most abundant nematode genera on the Fladen Ground were *Sabatieria*, *Aponema*, *Cyartonema*, and *Calomicrolaimus*. On the fishing ground in the Irish Sea, *Sabatieria*, *Aponema*, *Halalaimus*, and *Sphaerolaimus* were the most dominant genera. Nematode abundance, biomass, and production were over two times higher in the Irish Sea than in the North Sea (Fig. 2). Bottom trawling had a significant negative effect on nematode abundance, production, and genus richness in both areas (Table 3; Figs. 2*a*, 2*c*, 2*d*). Based on the results of the regression slopes in Fig. 2, a tenfold increase in trawling intensity from 1 to 10 $year^{-1}$ lead to a decrease in nematode abundance of 23.7% in the Irish Sea and 25.8% in the North Sea. Similarly, production was reduced by 25.7% and 16.3%, respectively. A tenfold increase in trawling intensity lead to a decrease in genus richness in the Irish Sea of 11.6%, while in the North Sea it decreased by 50.3%.

No significant effect of trawling frequency on nematode biomass was detected (Table 3, Fig. 2*b*). The interaction between trawling and area was significant for biomass and genus richness, indicating that the response to trawling within the two areas differed (Table 3, Fig. 2*d*).

In the North Sea, for three of the genera that were found in both areas, a significant response to trawling was detected. *Aponema* and *Sabatieria* had a positive response to increasing trawling frequency, while *Halalaimus* showed a negative response. The genera *Calomicrolaimus* and *Cyartonema*, which were not shared but were numerically important genera on the Fladen Ground, showed the following response: *Calomicrolaimus* (slope = –0.078; $r^2 = 0.66$; $p = 0.001$) and *Cyartonema* (slope = –0.002; $r^2 = 0.01$; $p = 0.906$). In the Irish Sea, three genera demonstrated a significant negative response to trawling: *Leptolaimus*, *Microlaimus*, and *Richtersia* (Table 3). Overall, 14 of the 20 showed obvious trends in response to trawling, most of

Fig. 2. The relationship between (*a*) abundance, (*b*) biomass, (*c*) production, and (*d*) genus richness with trawling frequency for nematodes. Significant regression lines are drawn ($p = 0.05$). Open circles indicate North Sea data; solid circles are data from the Irish Sea.

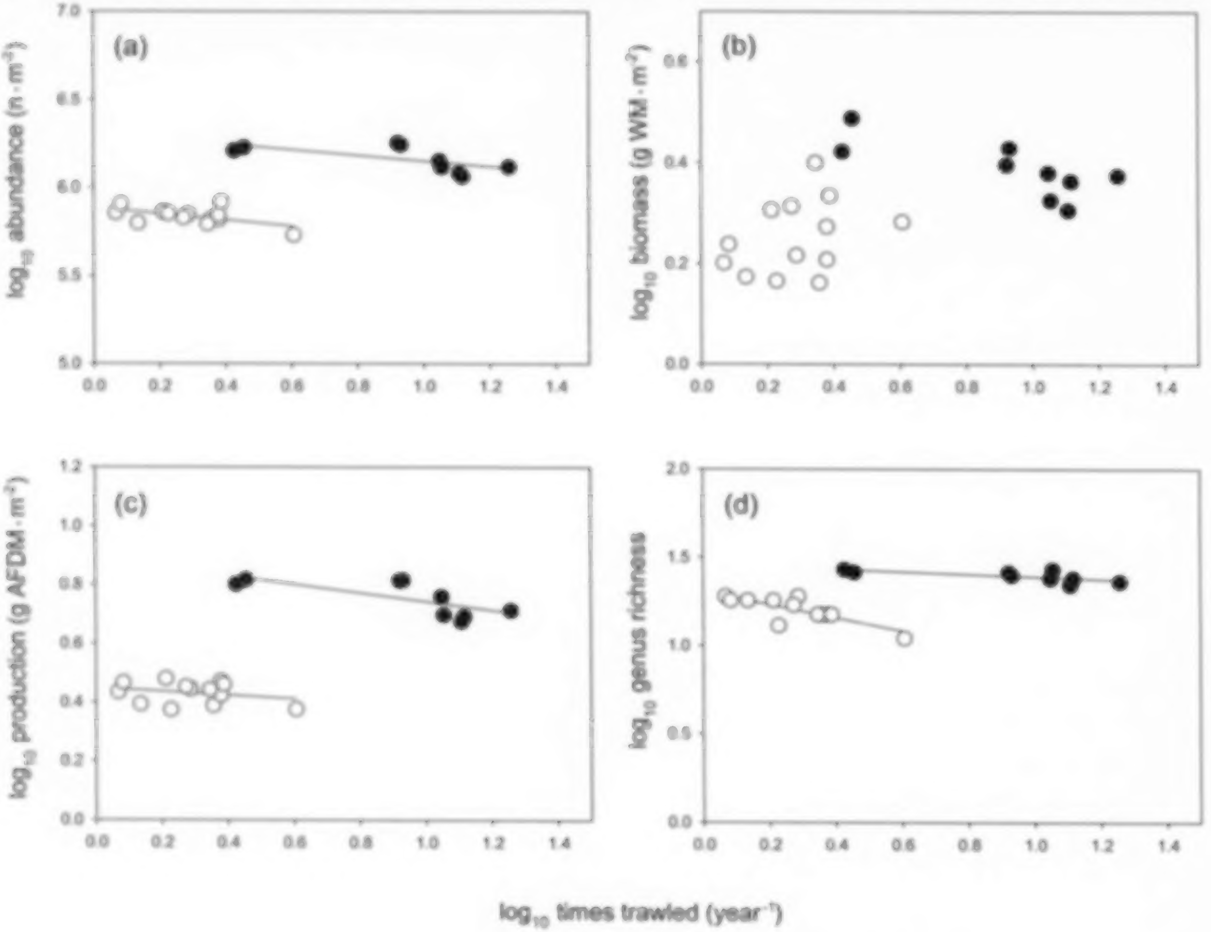


Table 3. Results of the generalized linear model analyses of the combined data from the North Sea and Irish Sea.

Dependant variable	Effect	$F_{[1,19]}$	p
$\log_{10}$ abundance ($n \cdot m^{-2}$)	Area	40.84	<0.001*
	$\log_{10}$ times trawled ($year^{-1}$)	8.89	0.008*
	Area × $\log_{10}$ times trawled ($year^{-1}$)	0.01	0.973
$\log_{10}$ biomass (g WM·m^{-2})	Area	15.28	0.001*
	$\log_{10}$ times trawled ($year^{-1}$)	0.01	0.924
	Area × $\log_{10}$ times trawled ($year^{-1}$)	5.23	0.034*
$\log_{10}$ production(g AFDM·m^{-2})	Area	66.26	<0.001*
	$\log_{10}$ times trawled ($year^{-1}$)	5.46	0.031*
	Area × $\log_{10}$ times trawled ($year^{-1}$)	1.12	0.383
$\log_{10}$ genus richness	Area	8.55	0.009*
	$\log_{10}$ times trawled ($year^{-1}$)	24.21	<0.001*
	Area × $\log_{10}$ times trawled ($year^{-1}$)	10.21	0.005*

Note: Dependant variables: univariate community descriptors (abundance, biomass, production, and genus richness). Independent variables: area (North Sea, Irish Sea) and fishing frequency (times trawled·$year^{-1}$). WM, wet mass; AFDM, ash-free dry mass; *, significant at $p = 0.05$.

which were in a similar direction. However, the number of genera that responded in a similar direction to trawling was not significantly higher than expected by chance (Fisher's exact test; $p = 0.17$).

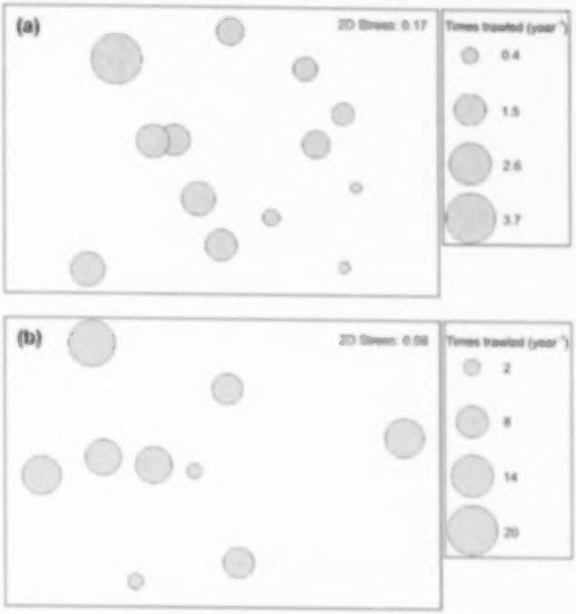
The MDS plots of the North Sea and the Irish Sea overlaid with trawling intensity as bubble plots only revealed a directional pattern for the North Sea (Fig. 3), which was confirmed by the seriation test (North Sea: $\rho = 0.42$, $p < 0.001$; Irish Sea: $\rho = 0.18$, $p = 0.24$). The BIOENV analysis of the North Sea showed that the ordination of the nematode community was best explained by four variables: trawling frequency, depth, silt–clay, and organic content of the sediment ($\rho_w = 0.452$), while the single factor that best explained the observed variation was trawling frequency, with a ρ_w of 0.418. The ordination of the Irish Sea data was best explained by two factors: bed shear stress and trawling frequency ($\rho_w = 0.313$). The single factor that best explained the observed variation was shear stress, with a ρ_w of 0.253 (trawling frequency $\rho_w = 0.178$).

Discussion

Chronic bottom trawling had a significant negative effect on nematode abundance, production, and genus richness within both study areas in the North Sea and Irish Sea. However, no significant response to trawling was detected for nematode biomass. Genus richness was more strongly affected by trawling in the Fladen Ground than in the Irish Sea. The reason for this difference is not clear, but could be related to an overall different community structure of the area surveyed in the Irish Sea. The sites investigated in the Irish Sea, compared with the ones in the North Sea, are exposed to higher shear stresses and thus may have favoured nematode species already tolerant to higher natural disturbance levels. Results of the multivariate analyses indicated that the community structure on a genus level was affected by trawling frequency in the North Sea but not in the Irish Sea.

The responses of individual nematode genera to trawling were not more similar between the two areas than could be expected by chance. Nevertheless, some similarities that were detected are further supported by the findings of previous studies. The abundance of the nematodes *Sabatieria* and *Aponema* increased significantly with trawling frequency in the North Sea, and similar trends, however nonsignificant, were detected in the Irish Sea. Earlier studies also have shown that these species increase under trawling disturbance (Schratzberger and Jennings 2002; Schratzberger et al. 2002). *Halalaimus* and *Calomicrolaimus* abundance was negatively affected by trawling in the North Sea, while in the Irish Sea *Halalaimus* was found to be unaffected by trawling. The negative response of *Halalaimus* to disturbance has not been documented before; on the contrary, *Halalaimus* seemed to thrive in disturbed sediments in microcosms (Schratzberger and Warwick 1998). A plausible explanation to these opposing findings has not been found to date. *Microlaimus* and *Richtersia* showed significant negative responses to trawling in the Irish Sea, and similar trends were observed for the North Sea (although not significant). *Microlaimids* are typically found in undisturbed sediments (Schratzberger and Warwick 1998) and are vulnerable to trawling effects (Schratzberger et al. 2002). Schratzberger et al. (2000) speculated that the negative effects of fishing on *Micolaimus* might be related to limited ability to migrate upwards when buried by sediment disturbance. Schratzberger and Jennings (2002) also recorded a negative response of *Richtersia* to trawling.

Fig. 3. Multidimensional scaling plot of nematode abundance data in (*a*) the North Sea and (*b*) the Irish Sea. Bubble sizes represent fishing intensities (times trawled·year^{-1}).



The mechanisms by which chronic trawling disturbance affects nematode communities are thus far not fully understood; however, they are most likely to be complex, and individual species can be expected to respond to different aspects of change induced by trawling. Owing to their small size, direct mortality from the physical impact of the trawling gear is unlikely to be important. Nevertheless, trawling may affect nematodes indirectly through affecting sediment composition and biological properties (e.g., biofilms on sediment particles) (Watling et al. 2001). Nematodes live in the interstitial spaces between sediment grains and therefore are thought to be susceptible to changes in sediment chemistry and composition. Trawling correlated positively with the water content of the sediment in the North Sea; this implied that the porosity of the sediment was greater under conditions of more intense trawling. These changes in sediment composition may have affected the nematode communities in the North Sea. Similar changes with increased trawling intensity were not detected in the Irish Sea, which might be related to the higher current regime within this area masking such changes. Generally, mixing of sediments and settling of resuspended matter following trawling disturbances can cause a vertical redistribution of sediment layers, which may have both positive and negative effects on nematodes (Mayer et al. 1991). Positive effects may arise from the re-release of buried organic material and nutrients from the redistribution of sedi-

Table 4. Linear relationships between nematode abundance and trawling frequency (times trawled·year^{-1}) for the genera that occurred within both areas in the North Sea and Irish Sea.

	North Sea			Irish Sea		
Taxon	Slope	r^2	p	Slope	r^2	p
Aponema	**0.065**	**0.46**	**0.006***	**0.025**	**0.05**	**0.276**
Axonolaimus	–0.009	0.00	0.555	–0.009	0.00	0.502
Daptonema	0.008	0.00	0.716	0.006	0.00	0.654
Desmoscolex	–0.011	0.00	0.335	0.008	0.00	0.567
Dorylaimopsis	0.007	0.00	0.728	–0.011	0.00	0.530
Halalaimus	**–0.042**	**0.35**	**0.019***	**0.005**	**0.00**	**0.591**
Laimella	–0.027	0.21	0.061	–0.005	0.00	0.462
Leptolaimus	**–0.021**	**0.02**	**0.288**	**–0.037**	**0.60**	**0.009***
Marylynnia	0.006	0.00	0.586	0.001	0.00	0.926
Mesacanthion	–0.006	0.00	0.727	–0.010	0.01	0.325
Microlaimus	**–0.012**	**0.14**	**0.114**	**–0.040**	**0.68**	**0.004***
Odontophora	0.026	0.06	0.208	–0.024	0.00	0.342
Paramesacanthion	0.041	0.16	0.095	–0.025	0.05	0.271
Richtersia	**–0.003**	**0.00**	**0.836**	**–0.042**	**0.56**	**0.013***
Sabatieria	**0.059**	**0.48**	**0.005***	**0.042**	**0.37**	**0.050**
Sphaerolaimus	–0.019	0.00	0.329	–0.026	0.28	0.084
Spirinia	–0.019	0.08	0.175	–0.012	0.09	0.227
Stephanolaimus	–0.018	0.11	0.146	–0.009	0.00	0.573
Terschellingia	–0.002	0.00	0.899	–0.035	0.15	0.163
Viscosia	–0.022	0.21	0.064	0.003	0.00	0.754

Note: Taxa showing a significant response in one of the two study areas are in bold type. *, significant at $p = 0.05$.

ments (Duplisea 2000), and species that are able to utilize this surplus of organic material may benefit. For example, the increase in abundance of *Sabatieria* with increasing trawling frequency, a nonselective deposit-feeder (Wieser 1953), may be explained by this. Similarly, increased organic loading of the sediment may lead to a shift towards microbial-dominated, anaerobic food chains (Brown et al. 2005), allowing only nematode species adapted to these conditions to survive. Furthermore, to understand the mechanics of chronic trawl disturbance on nematodes, the interdependence of bacteria and meio- and macro-faunal components in the benthic food web need to be acknowledged. Meiofauna and to some extend macrofauna depend on bacterial productivity, which in turn depends on the activity of the animals themselves, creating suitable conditions for bacterial growth (Gerlach 1978). Burrowing activities of meio- and macrofauna oxygenates the sediment, while their feeding activity fractionates larger organic particles in the form of faecal pellets, a substratum for bacterial growth. In addition, more sophisticated interactions exist in the form of species directly "gardening" bacterial growth (Gerlach 1978). Owing to this interdependence in benthic food webs, negative effects upon one faunal component can be expected to have an effect on the others. The direct, negative effect of trawling on macrofauna communities (Jennings and Kaiser 1998) thus may have an indirect negative effect upon nematodes by decreasing the suitability of the habitat to bacterial growth and thus ultimately food availability.

Overall nematode abundance, biomass, production, and the number of genera, as well as trawling frequency, was higher in the Irish Sea compared with the North Sea. The overall difference in the standing stock of nematodes within these two areas is most likely related to two possible factors: differences in local food supply and sampling in different seasons in the two areas. The Fladen Ground in the North Sea is characterized by relatively low primary productivity of 90–100 g C·m^{-2}·year^{-1} (De Wilde et al. 1986), while annual primary production off Cumbria is estimated at approximately 160 g C·m^{-2}·year^{-1} (K. Kennington, Scottish Environment Protection Agency, Clearwater House, Research Avenue North, Heriot Watt Research Park, Riccarton, Edinburgh EH14 4AP, United Kingdom, email: Kevin.Kennington@sepa.org.uk, personal communication). The higher primary production in the Irish Sea may at least partly explain the higher number and biomass of nematodes in the Irish Sea. On the Fladen Ground, sampling occurred during June when meiofauna abundances reach their seasonal low in this area (Faubel et al. 1983). In June, abundances are about half of those reached in December (seasonal peak). Sampling in the Irish Sea took place in November, and assuming a similar seasonal cycle for the meiofauna as for the Fladen Ground, meiofauna abundances may have been near their seasonal high, thus contributing to the differences observed between the two areas.

The results of this study clearly demonstrate that despite their small size and fast life cycle, nematodes are negatively affected by chronic trawling disturbance. Nematodes are thus not able to compensate for the loss in production by larger macrofauna as previously suggested (Jennings et al. 2001). Secondary production is thus further reduced by chronic trawling, with far-reaching consequences to the integrity of the benthic food web. Reductions within these groups may alter the pattern of energy flow through the marine ecosystem. Owing to the interdependence of bacteria and meiofauna and macrofauna production, the fate of unutilized benthic resources (such as particulate organic matter) in areas heavily defaunated by trawling remains unclear and needs further investigation.

As muddy seabeds cover over 50% of the earth's surface (Gage and Tyler 1991) and bottom trawl fisheries are expanding into ever deeper muddy habitats, the results presented in this paper are an important step towards understanding and assessing the global ecosystem effects of bottom trawling.

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Bomb radiocarbon chronologies in the Arctic, with implications for the age validation of lake trout (*Salvelinus namaycush*) and other Arctic species

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Abstract: Radiocarbon generated by atmospheric testing of nuclear weapons (bomb radiocarbon) produced a strong signal with an abrupt onset in the 1950s, which serves as a dated marker for tracing oceanic circulation and confirming age in animals forming growth bands. Here, we report the first prebomb and postbomb radiocarbon chronologies for marine and freshwater environments in the Canadian Arctic, extend the radiocarbon chronology for the northwest Atlantic Ocean, and use the onset of the bomb signal to validate our age interpretations of lake trout (*Salvelinus namaycush*) in Arctic lakes. Both surface and deepwater Arctic chronologies became detectable on or around 1958, similar to the year of onset elsewhere in the world. In contrast, the freshwater Arctic chronology increased sharply in 1957, with a peak value sixfold higher than the adjacent marine environment. The radiocarbon content of the adult otolith core validated our age interpretation criteria for Arctic lake trout to an age of at least 50 years. Otolith growth in such slow-growing fish was so low as to be unresolvable under conventional examination with a dissecting microscope. With these new radiocarbon reference chronologies, age validation of a large number of Arctic organisms should now be possible.

Résumé : Le radiocarbone généré par les essais atmosphériques d'engins nucléaires (radiocarbone de bombes) produit un fort signal qui apparait abruptement dans les années 1950 et qui sert de marqueur daté pour suivre la circulation océanique et pour confirmer l'âge chez les animaux qui portent des bandes de croissance. Nous présentons ici des chronologies au radiocarbone avant et après les essais nucléaires pour les environnements marins et d'eau douce de l'Arctique canadien; nous étendons cette chronologie au radiocarbone au nord-ouest de l'Atlantique et nous utilisons l'apparition du signal des bombes pour valider notre interprétation de l'âge de touladis (*Salvelinus namaycush*) dans des lacs arctiques. Les chronologies de l'Arctique, tant en eaux superficielles que profondes, sont devenues décelables en ou vers 1958, comme ailleurs dans le monde. En revanche, la chronologie arctique en eau douce accuse un net accroissement en 1957, avec une valeur du maximum six fois plus élevée que dans l'environnement marin adjacent. La concentration en radiocarbone du noyau des otolithes des adultes valide nos critères d'interprétation de l'âge chez les touladis arctiques jusqu'à l'âge d'au moins 50 ans. La croissance des otolithes chez ces poissons à développement lent est si faible qu'elle ne peut être interprétée par l'examen habituel à la loupe binoculaire. Ces nouvelles chronologies de référence de l'Arctique devraient permettre maintenant de valider la détermination de l'âge chez un grand nombre d'organismes arctiques.

[Traduit par la Rédaction]

Introduction

The atmospheric testing of atomic bombs in the 1950s and 1960s resulted in a rapid and well-documented increase in atmospheric radiocarbon, largely in the form of radioactive carbon dioxide, which first appeared around 1952 and peaked in 1964 (Nydal 1993). The exchange of radiocarbon between the atmosphere and precipitation was rapid and relatively complete, resulting in riverine and shallow freshwater radiocarbon values that peaked shortly after that of the atmosphere, albeit at lower concentrations (Peng and Broecker 1980; Spiker 1980). Peak values of bomb radiocarbon in the world's oceans were delayed until the late 1960s or 1970s as riverine input, precipitation, and atmospheric exchange of CO_2 gradually increased the concentration in surface marine waters (Druffel and Linick 1978). The exact year of peak radiocarbon and its rate of subsequent decline in the ocean was location-specific, because of the strong influence of water residence times, which affect the mixing of radiocarbon-depleted deep waters with bomb-enriched surface waters (Weidman and Jones 1993). However, the period of initial radiocarbon increase around 1958 was almost synchronous around the world and was recorded both directly in the water and measured in marine carbonate structures such as corals (Kalish 1995).

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Owing to its conservative nature, bomb radiocarbon has proven valuable as a chemical tracer in ocean circulation studies (Follows and Marshall 1996; Peng et al. 1998). Whereas surface marine waters equilibrated with the atmospheric bomb signal years ago, deep water that is upwelled has not been exposed to the bomb signal and therefore is depleted in radiocarbon. However, the tracer properties of bomb radiocarbon are not restricted to the water. Measurements of bomb radiocarbon in marine organisms have been used to trace the flow of carbon through the marine environment, such as the carbon flow from the surface waters to the deep sea (Pearcy and Stuiver 1983). All of these applications take advantage of the well-documented time series of the first appearance of bomb radiocarbon in temperate and tropical environments. This time series is so well understood that the appearance of bomb radiocarbon has proven very useful as a dated marker in any structures that form annual growth bands, such as trees (Worbes and Junk 1989), and in calcified structures such as corals, bivalves, and fish otoliths (Kalish 1993; Weidman and Jones 1993; Campana 1997).

Although the bomb radiocarbon chronology has been well characterized in temperate and tropical regions, it has not been well described in Arctic regions, particularly prior to 1979 (Ostlund et al. 1987). In large part, the absence of Arctic radiocarbon data is due to the absence of trees, corals, and bivalves in the Arctic, organisms that have provided detailed records of the radiocarbon chronology in other parts of the world. Isolated prebomb measurements based on growth bands in marine mammal bones and tusks have been reported (Tauber 1979; Bada et al. 1987), but the only continuous chronology for the Canadian Arctic across the 1950–1980 period is that based on beluga whale (*Delphinapterus leucas*) tooth growth bands (Stewart et al. 2006).

A promising alternative source of a radiocarbon chronology for the Arctic is that of fish otoliths, which have been used extensively for this purpose in other parts of the world (Campana 2001). Otoliths share a number of favourable properties with other radiocarbon proxies such as corals and bivalves: long-term stability, annual growth bands that can be aged and dated, and a radiocarbon content that is representative of the dissolved inorganic carbon (DIC) of the water in which the fish lived (Kalish 1995). In a recent study, Kalish et al. (2001) derived an extensive radiocarbon chronology for the surface waters of the Barents Sea based on annual growth bands isolated from Atlantic cod (*Gadus morhua*) otoliths. A comparable chronology does not yet exist for the terrestrial Arctic or marine waters of the Canadian Arctic, but would be particularly valuable for future studies of the age determination of terrestrial, freshwater, and marine Arctic organisms.

Bomb radiocarbon chronologies can also be used to validate the age and growth of many long-lived animals, including fish. The growth rates of fish in the Arctic would be expected to be very low, because of both low temperatures and low nutrient levels (Power 1997). Surprisingly however, there has been no independent confirmation of growth rate or age interpretation in any Arctic fishes other than Arctic grayling (*Thymallus arcticus*) (DeCicco and Brown 2006). This is particularly true for Arctic fishes believed to be long-lived, since traditional length frequency analyses are not effective for fish more than a few years old. In addition, many published age and growth interpretations of Arctic fishes are based on traditional surface readings of scales or otoliths, methods that are now known to underestimate (sometimes grossly) the age of long-lived fishes (Casselman 1987; Campana 2001). Johnson (1976) was the first to report that lake trout (*Salvelinus namaycush*) in the Arctic appear to be long-lived; however, his use of surface otolith readings left open the possibility that they were even longer-lived and slower-growing than he suspected. This possibility was tentatively confirmed by Power (1978), whose use of otolith transverse sections resulted in lake trout age estimates >50 years in some fish. While Power (1978) expressed doubt about the accuracy of previous ageing studies and confidence in his more modern ageing methods, he acknowledged that confirming his age interpretations would prove to be difficult or "impossible". However, recent technological advancements using bomb radiocarbon now make such age validations possible (Campana 2001).

The first objective of this study is to document the magnitude and timing of the bomb radiocarbon signal in the Canadian Arctic, both in freshwater and ocean environments. We will then contrast these Arctic radiocarbon chronologies with those from more temperate locations. A second objective is to use the bomb radiocarbon chronologies to validate an ageing method for lake trout in Arctic lakes, thus setting a basis for validating the ages of other Arctic organisms, both in fresh water and salt water.

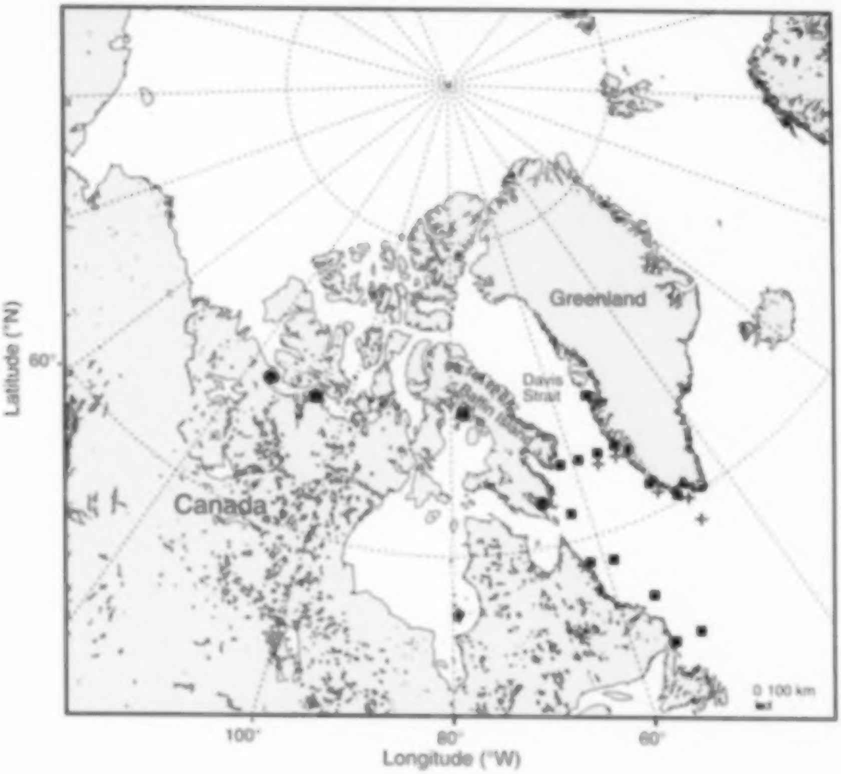
Materials and methods

Reference chronologies

All reference chronologies were based on archived collections of young fish otoliths whose age was either known or could be estimated based on their length. The very distinct length modes in the collections of these young fish suggested that actual age was unlikely to differ from estimated age by more than ±1 year.

The reference $\Delta^{14}C$ carbonate chronology for the Northwest Atlantic (NWA) was derived from 56 sagittal otoliths extracted from haddock (*Melanogrammus aeglefinus*) and redfish (*Sebastes* spp.) of ages 1–3 years from southern Newfoundland (North Atlantic Fisheries Organization (NAFO) Division 3Ps) whose cores were formed between 1949 and 1982 (Campana 1997; Campana et al. 2002). An additional 17 samples of age 1–2 haddock and yellowtail flounder (*Limanda ferruginea*) otoliths were collected from 3Ps between 1980 and 2000 and prepared in a similar manner. Graphically, the $\Delta^{14}C$ chronologies of the three species were indistinguishable, nor was a difference expected given the common depth and environment during the first few years of life. An analysis of variance (ANOVA) of the detrended residuals from a species-combined chronology demonstrated that there were no significant differences among the species; the statistical power of this test to detect an interspecies difference corresponding to about 1 year (a $\Delta^{14}C$ of 11) was 70% for the period of increasing $\Delta^{14}C$ values (1950–1970) and 96% for 1.5 years. Given the absence of interspecies differences, the species were pooled, averaged within years, and used as a single chronology. The prebomb chronology was supplemented by three published $\Delta^{14}C$ values from a bivalve on Georges Bank for the years 1939–

Fig. 1. Map indicating collection sites for bomb radiocarbon reference chronologies of freshwater *Salvelinus alpinus* (●), marine *Gadus ogac* (+), and marine *Reinhardtius hippoglossoides* (■).



1946 (Weidman and Jones 1993). The $\Delta^{14}C$ chronologies of aragonitic fish otoliths and bivalves in the NWA are indistinguishable during the prebomb era (before 1958) and begin to increase at virtually identical times (Campana 1997); thus the NWA chronology is a good proxy for the $\Delta^{14}C$ DIC history of the NWA.

The Greenland cod (*Gadus ogac*) reference chronology represents the surface marine waters of Davis Strait and western Greenland. The chronology was derived from 46 samples of age 0–3 *G. ogac* otoliths collected between 1954 and 2000 from NAFO Divisions 1CDEF (eastern Davis Strait) and stored dry in paper envelopes at the Gronlands Naturinstitut in Greenland (Fig. 1).

The Greenland halibut (*Reinhardtius hippoglossoides*) reference chronology represents the $\Delta^{14}C$ of the deeper waters (200–800 m with an average depth of 300 m) of Davis Strait and western Greenland. The chronology was derived from 38 samples of age 0–3 (<30 cm) *R. hippoglossoides* collected with otter and prawn trawls from NAFO Divisions 0B (western Davis Strait), 1ABCEF (eastern Davis Strait), and 2G and 2J (northern Labrador) on Danish, German, or Canadian surveys (Treble et al. 2008) (Fig. 1). The otoliths were stored dry in paper envelopes at the Gronlands Naturinstitut in Greenland or at the Northwest Atlantic Fisheries Centre in Newfoundland. Otolith cores from an additional three large (66–89 cm) adult Greenland halibut collected from NAFO Divisions 1EF and 2G in 1962–1966 were assayed to characterize the prebomb environment (Treble et al. 2008). Although the exact age of these adult fish was not known, we are confident that they were at least 10 years old, implying that their otolith cores were formed prior to 1958.

The reference chronology for the freshwater environment in the Arctic was largely based on Arctic char (*Salvelinus alpinus*) collections made in the 1960s by Lionel (Jim) Johnson; these otoliths were stored at the Arctic Institute in Ste-Anne-de-Bellevue, Québec, and subsequently transferred to the Canadian Museum of Nature, where they were accessed. The otoliths used in this study consisted of 58 samples of age 0–5 Arctic char collected between 1957 and 1969 throughout the Canadian Arctic north of latitude 62°50′ (Fig. 1). The mean length of the char was 10 cm (range of 7–21 cm), and the mean age was 2.8 years. Since the otoliths were quite small (0.4–4 mg per pair), otolith pairs were pooled across 1–10 fish of the same age and comparable length for assay. By pooling otoliths across fish, we have implicitly assumed that there is no ageing error for these young fish. Although we have no way to test this assumption, the length modes for these young fish were sufficiently distinct that it appears unlikely that our age estimates were in error by more than ±1 year.

The feature of a bomb radiocarbon chronology that is most stable across locations and environments is the year of initial increase above prebomb levels in response to the period of atmospheric testing of nuclear weapons. In surface marine chronologies in temperate and tropical environments, it is generally accepted that the bomb signal first became visible around 1958 (Druffel and Linick 1978; Kalish 1995). However, there has been little agreement among authors on how the year of first increase is to be determined in a new chronology. Past studies have used graphical interpretation of the Δ^{14}C chronology (Kalish 1993; Campana 1997) or calculation of the year that first exceeds the 95% confidence interval of the Δ^{14}C of the prebomb years after fitting a curvilinear equation to the Δ^{14}C chronology (Kerr et al. 2004; Stewart et al. 2006). Although both approaches are well intentioned, the graphical interpretation is subjective and the years selected for entry into the curvilinear fit are arbitrary. Therefore, we adopted a quantitative but simple approach for defining the year of initial increase, based on bomb input values into the atmosphere. Naegler and Levin (2006) documented bomb radiocarbon inventories for the atmosphere, ocean, and biosphere as part of a global bomb radiocarbon budget. The total cumulative radiocarbon input from nuclear bombs and the nuclear industry increased from about 0 in 1952 to 580 × 10^{26} atoms ^{14}C near its peak in 1963 for an average of 52.7 × 10^{26} atoms ^{14}C annually. This corresponds to an annual increase of 9.1%·year^{-1} and is approximately equal to the annual increase between 1954 and 1955, shortly after atmospheric testing of nuclear weapons began. A comparable pattern exists in both the modelled (Naegler and Levin 2006) and observed (Campana 1997) ocean ^{14}C inventories, with an average increase of 9%–10% per year between prebomb and peak Δ^{14}C levels, although the initial increase in the ocean did not become evident until about 1958. Therefore, it appears that a Δ^{14}C value 10% above the prebomb background is a valid indicator of the year of initial appearance of bomb Δ^{14}C and one that is consistent with atmospheric sources. However, estimation of a suitable prebomb background is not necessarily straightforward. Therefore, we based our calculation on the difference in Δ^{14}C values between the peak and prebomb values, which is easily and unambiguously calculated. Specifically, we estimated the value corresponding to the 10% threshold contribution of Δ^{14}C (C_T) by calculating 90% of the range in Δ^{14}C between its lowest (C_L) and peak (C_P) value and subtracting it from the peak value, as in

$$C_T = C_P - 0.9(C_P - C_L)$$

where C_L is on or after 1952, the year of initial appearance of bomb radiocarbon in the atmosphere. The year of initial appearance of bomb Δ^{14}C (Y_T) is then defined as the year in which the Δ^{14}C chronology first exceeds C_T.

We tested the accuracy of Y_T as a measure of year of initial appearance of bomb Δ^{14}C by applying it to all published marine bomb radiocarbon chronologies. In all cases, the calculated Y_T value lay in the range of 1957–1960, except where sample spacing did not allow more precise estimation (e.g., 1955–1960 for Kalish 1993). The advantage of this measure of Y_T over other methods is that it is relatively insensitive to random variation in prebomb values and is not based on an arbitrary selection of years for estimation. Therefore, it appears suitable for use in bomb radiocarbon studies in general.

Age validation

Otolith cores removed for age validation were collected from subadult and adult lake trout collected from Tasiat Lake (59°10′N, 75°16′W) and Lac Couture (60°08′N, 75°25′W) in the eastern Arctic in 2002 and from Zeta Lake (71°06′N, 106°34′W) in the western Arctic in 2003.

All ages were based on counts of presumed annual growth increments that were visible in transverse sections of the sagittal otolith. Otoliths to be aged were first embedded in a slow-drying hard epoxy (Araldite epoxy GY502 and hardener HY956 in a 5:1 weight ratio). Sections through the core (~450 μm thickness) were prepared with a single cut using twin blades separated by a spacer on an Isomet low-speed, diamond-bladed saw. The sections were subsequently mounted on a standard microscope slide with a thin coat of epoxy, then lightly polished to improve visibility. While under a binocular microscope at 16–40× magnification using reflected light, the growth increment sequence was digitally photographed at a resolution of 1280 × 1024, then digitally enhanced for contrast using Adobe Photoshop CS2. Age interpretation was based on the enhanced images. In the case of lake trout believed to be older than 30 years, a second set of age readings was made under transmitted light using a compound microscope at magnifications of 160× with no imaging. Bias between ageing methods was evaluated with age bias plots, whereas precision was quantified using the coefficient of variation (CV) (Campana 2001).

Otolith cores for bomb radiocarbon age validation were isolated from three adjacent 1.2 mm thick transverse sections of the otolith, polished lightly to view the growth sequence. Otolith cores representing the first 3 years of life were isolated from the central section as a solid piece with a Merchantek computer-controlled micromilling machine using 300 μm diameter steel cutting bits and burrs. Additional core material from the same otolith was isolated from the two adjacent sections, but restricted to the innermost two growth increments so as to allow for the offset of these lateral sections from the primordium. This procedure of obtaining material from multiple sections per otolith was necessary to maximize the amount of sample material available for assay from each otolith. Even then, the mean weight of isolated core material was ~0.5 mg. Therefore, otolith cores from 1–10 additional fish of the same age and similar length were extracted and pooled so as to bring the sample weight up to the minimum of 3 mg necessary for radiocarbon assay. By pooling otolith material across fish, we may have introduced variance into the estimate of year of core formation, but this was unavoidable. The date of sample formation was calculated as the year of fish collection minus the age span of the fish from the edge of the otolith to the midpoint of the range of growth increments present in the extracted core. After sonification in Super Q water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). AMS assays also provided δ^{13}C (‰) values, which were used to correct for isotopic fractionation effects and provide information on the source of the carbon. Radiocarbon values were subsequently reported as Δ^{14}C, which is the per mil (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay prior to 1950 according to methods outlined by Stuiver and Polach (1977).

The mean standard deviation of the individual radiocarbon assays was about 5‰.

Results

Reference chronologies

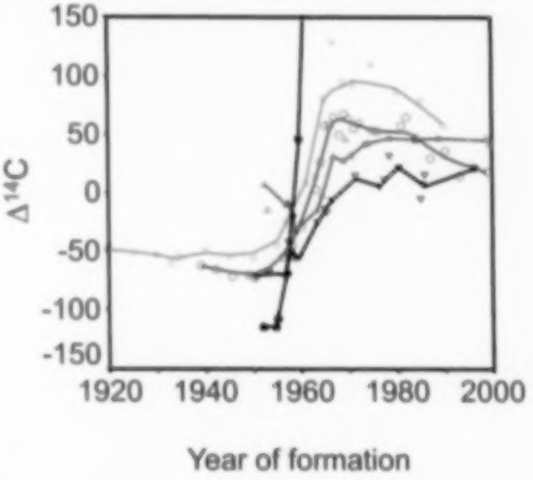
Despite the broad range of habitats that they represent, the four reference chronologies all showed similar and characteristic bomb radiocarbon patterns: relatively low $\Delta^{14}C$ prior to 1957, a sharp increase during the 1960s, and stable or gently declining values after 1970 (Fig. 2; Table 1). Prebomb values (prior to 1957) were virtually identical at a $\Delta^{14}C$ of about −70 in the NWA and Arctic deepwater (Greenland halibut) chronologies. In contrast, the prebomb chronology for the surface marine Arctic (*G. ogac*) was markedly less depleted than the other chronologies prior to 1958, a finding that was sufficiently surprising that it prompted a reanalysis of additional samples, but with no change. The prebomb $\Delta^{14}C$ value of −114 in the freshwater Arctic chronology (Arctic charr) was markedly more depleted than any of the other chronologies.

$\Delta^{14}C$ levels after 1970 differed substantially among all of the chronologies. Peak $\Delta^{14}C$ levels were reached around 1966 in the case of the Arctic freshwater chronology, around 1969 for the NWA, and in the late 1970s for the two Arctic marine chronologies (Table 1).

The feature of a bomb radiocarbon chronology that best serves as a dated reference mark is the year of initial increase above prebomb levels in response to the period of atmospheric testing of nuclear weapons. In the three marine reference chronologies reported here, this period of initial increase was calculated to lie between 1957 and 1959 in all cases. The NWA and deepwater Arctic marine chronologies began to increase in 1957, while the surface marine chronology began 2 years later in 1959 (Fig. 2; Table 1). In contrast, the freshwater Arctic chronology increased sharply in 1957, much more abruptly than the others.

The Arctic freshwater radiocarbon chronology clearly differed from that of the other habitats, both with respect to period of increase, prebomb $\Delta^{14}C$, and peak $\Delta^{14}C$ (Fig. 2). Comparison of the freshwater pattern with the atmospheric $\Delta^{14}C$ chronology documented by Nydal (1993) indicates that the freshwater $\Delta^{14}C$ signal closely resembled an attenuated version of the atmospheric chronology. Both time series began to increase in earlier years and reached much greater peak values than did the NWA or other marine chronologies (Fig. 3). Indeed, the peak $\Delta^{14}C$ values in the freshwater environment were so much greater than those of the marine environment that environment type was easily identifiable in otolith samples collected in the mid-1960s.

Fig. 2. Bomb radiocarbon reference chronologies for Arctic fishes based on $\Delta^{14}C$ incorporated during the first few years of growth into young, known-age fish otoliths. While the prebomb (before 1958) and postbomb (after 1970) $\Delta^{14}C$ values differ among species, the period of increasing values is very similar in all of the marine time series and thus can be used as a dated marker. Fitted lines are locally weighted least square (LOESS) regressions. Freshwater *Salvelinus alpinus*, black solid circles; marine *Gadus ogac*, green open triangles; marine *Reinhardtius hippoglossoides*, blue inverted open triangles; marine Northwest Atlantic reference chronology, red open circles; marine *Gadus morhua* (Kalish et al. 2001), light blue open squares.



Otolith growth patterns of lake trout

Growth increments, presumed to be formed annually, were clearly visible under reflected light in at least some regions of all of the otolith sections examined. In most otoliths up to an apparent age of about 20 years, one or several growth axes appeared to contain complete growth sequences, particularly those leading from the core to the dorso-proximal or ventro-proximal surfaces (Fig. 4). In older fishes, however, the number of increments visible along the growth axis often differed with the transect selected for ageing. In general, the clarity and spacing of the growth increment sequence was optimized in the thickened dorsal lobe (proximal surface) immediately adjacent to the sulcus (Fig. 4). Growth increments were also often interpretable in the ventral lobe (proximal surface) immediately adjacent to the sulcus, but sometimes produced an increment count 1–2 years less than that of the dorsal lobe. Growth increments did not appear to form consistently after an age of 20–30 years towards the ventral or dorsal tips, despite the fact that these axes were often the longest in the section.

Difficulties in resolving growth increments first became apparent at an age of 40–45 years towards the edge of the otolith (Fig. 5*a*). This region of the otolith was often characterized by a regular sequence of increments of gradually decreasing width that eventually became almost featureless, even after aggressive image enhancement at a magnification of 40×. Visibility was not improved appreciably under transmitted light using the same microscope. However, after the section was polished to a smooth surface, the growth increments became very clear when examined with transmitted light under a compound microscope at 160× (Fig. 5*b*). Increment width near the proximal surface of old fish could be as narrow as 20 μm, which probably explains the difficulty in viewing the individual increments under a binocular microscope.

To insure that the increments visible using transmitted light under the compound microscope were comparable to those visible using reflected light under the binocular microscope after image enhancement, a series of 107 otoliths were

Table 1. Summary of $\delta^{13}C$ (‰) and $\Delta^{14}C$ assay results for young Arctic fish otoliths used in the preparation of reference chronologies.

	Salvelinus alpinus		*Gadus ogac*		*Reinhardtius hippoglossoides*		NWA reference	
Year of formation	$\delta^{13}C$	$\Delta^{14}C$	$\delta^{13}C$	$\Delta^{14}C$	$\delta^{13}C$	$\Delta^{14}C$	$\delta^{13}C$	$\Delta^{14}C$
1939.0								−61.3
1942.0								−64.4
1945.5								−70.6
1947.5					−1.1	−71.0		
1949.0							−2.7	−68.8
1950.0							−3.6	−71.8
1950.5					−1.9	−66.3		
1952.0	−2.3	−114.0						
1952.5			−1.2	7.7				
1953.0			−2.1	−13.6			−1.8	−67.3
1954.5	−7.6	−113.7						
1955.0	−7.5	−106.6						
1956.0							−3.0	−54.5
1956.5					−2.2	−69.7		
1957.0	−11.6	−68.3	−2.3	−8.9				
1957.5			−2.0	−7.3	−2.8	−41.1		
1958.0	−10.0	−19.0			−3.1	−49.1	−3.4	−53.0
1958.5			−1.2	−42.4				
1959.0			−2.0	−31.2	−2.9	−54.8		
1959.5	−8.8	45.9			−3.1	−54.2		
1960.0							−2.1	−27.8
1962.5	−6.9	309.7						
1963.0	−7.0	287.7					−1.1	3.6
1963.5	−6.9	335.5	−2.2	−13.5	−3.5	−24.5		
1964.0							−3.4	26.4
1964.5			−1.9	−1.4				
1965.0					−3.0	−13.0	−3.8	58.9
1965.5					−2.6	−15.7		
1966.0							−4.3	58.2
1966.5	−7.6	383.4			−2.8	−5.6		
1967.0	−6.8	369.4	−1.8	31.0			−3.9	65.5
1968.0							−2.6	50.6
1969.0			−2.5	27.9			−1.9	68.0
1969.5			−3.6	46.2				
1970.0							−1.4	63.7
1970.5			−1.8	31.7				
1971.0							−2.2	55.9
1971.5					−2.6	15.1		
1972.0							−1.3	60.4
1973.5			−2.0	41.8				
1974.0			−2.7	42.7				
1975.0							−0.5	53.9
1976.0							−1.5	52.8
1976.5					−2.8	6.3		
1977.5					−2.9	12.1		
1978.5			−1.7	46.8	−2.5	31.8		
1980.5					−2.9	22.8		
1981.0							−1.6	58.2
1982.0							−0.7	65.9
1984.0			−2.7	45.0			−2.4	47.6
1985.0					−2.3	−4.1		
1985.5					−3.3	8.0		
1986.5					−2.8	16.4		
1987.0							−1.1	30.3
1989.0			−2.0	47.5				

Table 1 (*concluded*).

Year of formation	*Salvelinus alpinus* $\delta^{13}C$	*Salvelinus alpinus* $\Delta^{14}C$	*Gadus ogac* $\delta^{13}C$	*Gadus ogac* $\Delta^{14}C$	*Reinhardtius hippoglossoides* $\delta^{13}C$	*Reinhardtius hippoglossoides* $\Delta^{14}C$	NWA reference $\delta^{13}C$	NWA reference $\Delta^{14}C$
1990.0							–2.5	36.5
1993.0							–2.2	15.4
1996.0							–3.2	22.6
1996.5					–3.2	21.3		
1999.0			–2.3	48.1			–2.6	19.3
1999.5			–3.2	41.9				
2000.5							–2.8	33.7

Note: The Northwest Atlantic (NWA) reference chronology is composed of three fish species from the eastern coast of Canada; samples prior to 1946 are values reported by Weidman and Jones (1993) for east coast bivalves.

Fig. 3. The $\Delta^{14}C$ reference chronology for a freshwater Arctic species (●) more closely resembles the atmospheric time series (adapted from Nydal 1993) than the marine Northwest Atlantic (NWA) time series, with an earlier period of increase and higher peak values than the marine reference chronology. Fitted solid lines are locally weighted least square (LOESS) regressions, while the broken line is an interpolated fit.

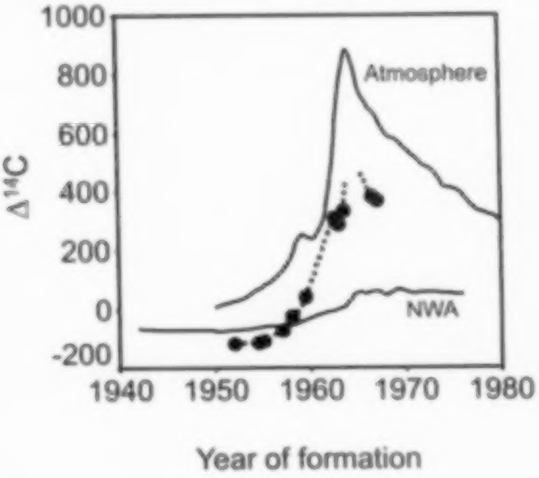
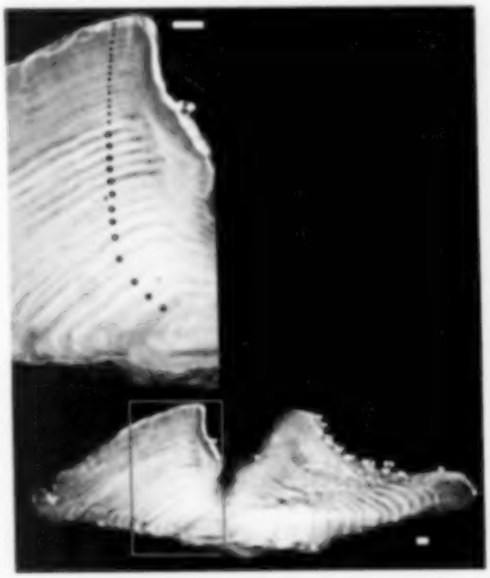


Fig. 4. Annual growth increments in a transverse otolith section of a 56 cm, 29-year-old lake trout (*Salvelinus namaycush*) from Tasiat Lake. Inset shows the axis used for age determination and annotated growth increments. The image has been contrast-enhanced. Scale bar = 100 µm.



independently aged under both microscopes. An age bias plot indicated that there was no bias between the two viewing procedures until an age of about 45 years (Fig. 6). The precision (CV) between the ageing methods for these unbiased ages was 4.6%. At ages greater than 45 years, more increments were consistently seen under the compound microscope (Fig. 6). There were 63 otoliths aged as being over 45 years of age using the compound microscope for which reflected light increment counts were not possible because of poor visibility of the most recently formed growth increments.

Age validation of lake trout

The date of formation of the lake trout otolith cores was estimated in two ways: through age determination of the fish based on otolith growth increment counts and through comparison of otolith core $\Delta^{14}C$ values with the values known to be present in the Arctic freshwater environment at the time (the Arctic freshwater reference chronology). Where the increment-based and $\Delta^{14}C$-based dates are in agreement, the increment-based age interpretations must be (on average) correct.

The correspondence between the Arctic freshwater reference chronology and the chronology derived from the lake trout otolith cores was very close (Fig. 7). Both chronologies describe a curve that closely resembles an attenuated version of the atmospheric chronology (Fig. 3), with a rapid increase between 1957 and the late 1960s, followed by a gradual decline through to 1995. The key samples for comparison were the cores formed before 1962 (Table 2), since they were formed during the period when environmental ^{14}C levels changed most rapidly. The core that was formed during the 1940s, and that was 62 years old based on increment counts, was clearly a prebomb value based on $\Delta^{14}C$ and thus must

Fig. 5. Growth increments near the otolith margin in a transverse section of a 46-year-old lake trout (*Salvelinus namaycush*) otolith are less visible in a reflected light image (*a*) than in a transmitted light image (*b*), largely because of the narrow width of the growth increments. Both images have been digitally enhanced to the same extent. Scale bar = 100 µm.

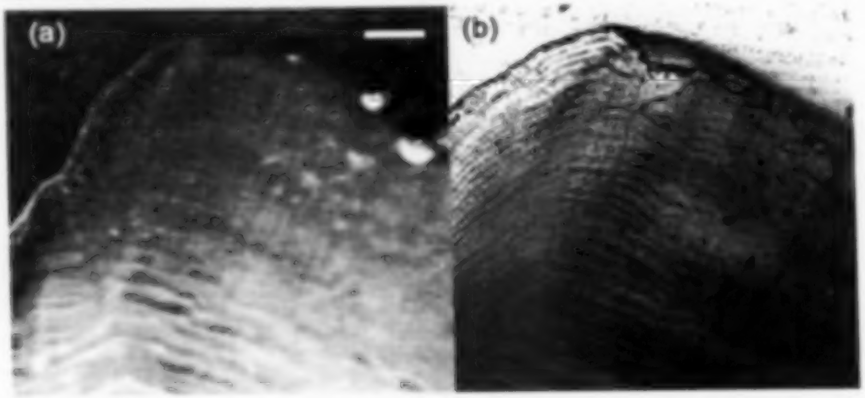


Fig. 6. Age bias plot comparing lake trout (*Salvelinus namaycush*) age estimates using a compound microscope and transmitted light with a stereomicroscope and reflected light. Deviation of mean ± 95% confidence interval bars from 1:1 line at older ages indicates that reflected light increment counts increasingly underestimate ages of trout older than about 45 years. An additional 63 otoliths (Δ) from fish over 45 years of age (using the compound microscope and transmitted light) could not be aged under reflected light, because of poor visibility of the most recently formed growth increments.

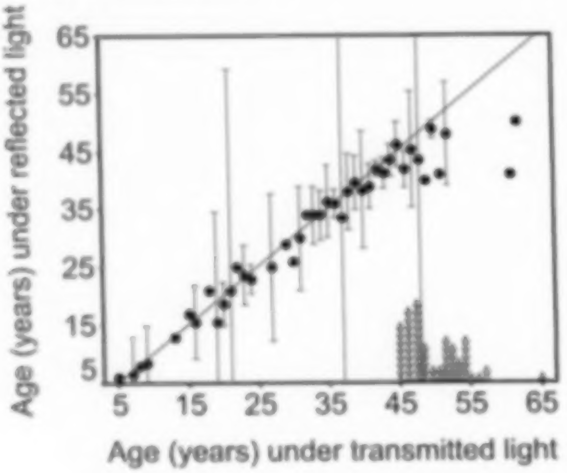
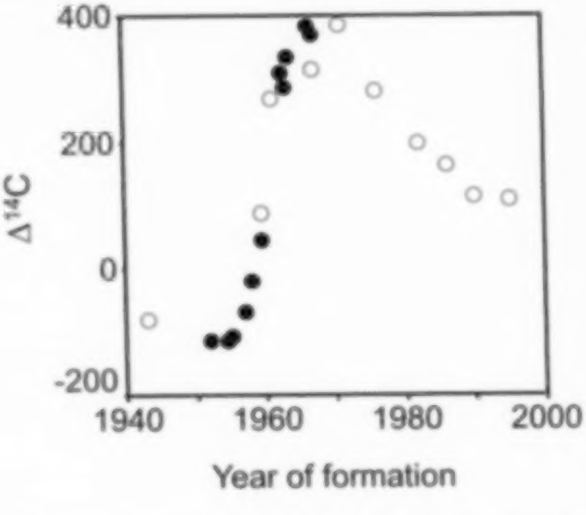


Fig. 7. $\Delta^{14}C$ in otoliths of young known-age Arctic char (*Salvelinus alpinus*) (●) and cores of old lake trout (*Salvelinus namaycush*) (○) versus year of formation inferred from counts of the growth increments. The correspondence between the two radiocarbon chronologies indicates that the ages of the older lake trout were relatively accurately interpreted based on the growth increment counts.



have been at least 50 years old (Table 2). Two other core samples, dated as having formed between 1960 and 1961 based on increment counts of 42–45 years, were dated by $\Delta^{14}C$ as having formed between 1960 and 1961, with a maximum uncertainty of about 2 years. Therefore, these results clearly validate the interpretation of the lake trout otolith increments as accurate age indicators to an age of at least 45 years and longevity of at least 50 years.

The core samples dated as forming between 1970 and 1995 closely resemble the declining bomb radiocarbon levels in the atmosphere during those years, but lagged by several years compared with the period of increase (Table 2; Fig. 7). The lagged pattern is that expected of recycled carbon in a living aquatic system and underlines the importance of using the period of increasing radiocarbon levels as a dated marker rather than the subsequent decline.

Discussion

The Arctic radiocarbon chronologies all showed the generic bomb signal characteristic of other regions around the world: relatively low $\Delta^{14}C$ prior to 1957, a sharp increase during the 1960s, and stable or gently declining values after 1970. However, there were subtle differences among the marine chronologies and more prominent differences be-

Table 2. Summary of δ^{13}C (‰) and Δ^{14}C assay results for otolith cores (3 years of growth) microsampled from Arctic lake trout (*Salvelinus namaycush*) for age validation.

Sampling site	Year collected	Age (years)	Year of core formation	No. of cores	δ^{13}C	Δ^{14}C
Tasiat–Couture	2002	8	1995	11	−11.9	110.4
	2002	13–14	1989–1990	11	−10.9	115.7
	2002	17–18	1985–1986	12	−10.3	163.4
	2002	21–23	1980–1982	10	−10.1	198.6
	2002	27–28	1975–1976	9	−9.8	282.4
	2002	32–34	1969–1971	13	−9.4	385.1
	2002	36	1967	4	−10.4	314.7
	2002	42	1961	3	−9.8	270.0
Zeta	2003	44–45	1960–1961	5	−4.5	88.6
	2003	62	1942–1946	1	−4.3	−80.7

Note: Year of core formation is that based on the number of growth increments.

tween the freshwater and marine chronologies. Compared with the marine chronologies, the two freshwater chronologies were more depleted (by a Δ^{14}C of about −44) during prebomb years, first showed evidence of a strong bomb signal somewhat earlier, and reached a peak Δ^{14}C at least sixfold higher. These freshwater characteristics reflect a slightly muted atmospheric radiocarbon signal, thus emphasizing the strong influence of atmospheric input of radiocarbon into terrestrial (including freshwater) systems. The contrast in prebomb and peak radiocarbon values between the freshwater and marine systems was so strong that it was easy to distinguish the habitat type of the target species based only on the radiocarbon chronology of the otolith; this was even more evident when done in concert with the more depleted δ^{13}C values that were characteristic of the freshwater fish otoliths. There are no other published freshwater radiocarbon chronologies for comparison. However, the estuarine radiocarbon signal derived from otolith cores of black drum (*Pogonias cromis*) was very similar to the freshwater Arctic chronology, both in terms of timing and peak values (Campana and Jones 1998).

The differences among the various Arctic marine chronologies were more subtle, apparently reflecting their environments. The prebomb Δ^{14}C value of about −70 in the Arctic deepwater (Greenland halibut) chronology was only marginally different than the prebomb value of −54 reported by Kalish et al. (2001) for Arcto-Norwegian Atlantic cod (*G. morhua*) off of east Greenland. Ostlund et al. (1987) reported Δ^{14}C values of about −46 for the surface waters of the East Greenland Current in 1957, but noted that there was no radiocarbon data available for the Arctic Ocean prior to 1979. The only other prebomb values available for the Arctic are those based on marine mammal hard parts: Δ^{14}C of −58 to −71 from marine mammal bones (Tauber 1979) and a Δ^{14}C of about −80 from beluga whale teeth (Stewart et al. 2006). In contrast, the prebomb Δ^{14}C values of around zero from our surface marine Arctic chronology (Greenland cod) were markedly less depleted than the other chronologies. Although we are satisfied (through repeat assays) that the relatively high prebomb values in the Greenland cod assays are not due to analytical error, we are at a loss to explain Δ^{14}C values that apparently declined substantially in the 6 years predating the appearance of the bomb signal in 1959. Natural variability in the background Δ^{14}C signal has been documented in tree ring chronologies (Levin and Hesshaimer 2000), but the magnitude of this variability is somewhat less than what was observed in the prebomb surface marine Arctic chronology. Nevertheless, the initial appearance of the bomb signal between 1957 and 1959 in the two Arctic marine chronologies was relatively similar, despite the fact that the deep-sea chronology would have been expected to be delayed relative to that in surface waters. No such delay was evident, perhaps because of rapid transport of dissolved organic carbon and particulate organic carbon from the surface to the depths at which the Greenland halibut lived (Pearcy and Stuiver 1983; Williams et al. 1987). Indeed, many of the postbomb values in the deep-sea chronology were only slightly above zero, a Δ^{14}C reference level that often distinguishes clearly between prebomb and postbomb dates in other environments. Since a postbomb Δ^{14}C value of zero is more characteristic of depths of 500–1000 m in Arctic waters (Schlosser et al. 1994), the young Greenland halibut used to develop the deep-sea chronology may have lived at greater depths than indicated by their 300 m mean depth of capture. Differences in Δ^{14}C values after 1970 among the chronologies was expected given the very different water mixing times of the various habitats (Kalish 1995) and a latitudinal gradient in surface water Δ^{14}C of about 100 between the maximum at 30°N and a minimum at about 60°N (Levin and Hesshaimer 2000).

The radiocarbon assays reported in this study, that of cod by Kalish et al. (2001), and that of Greenland halibut by Treble et al. (2008) form the only available reconstructions of the bomb radiocarbon chronology for the Arctic. Presumably, the prior absence of these chronologies in the Arctic is due to the absence of recent trees and corals, upon which most chronologies are based. Licht et al. (1998) studied bomb radiocarbon in Arctic marine sediments, but no link to water-borne values was made. Bada et al. (1987) presented what they believed to be a prebomb and postbomb radiocarbon chronology based on narwhal (*Monodon monoceros*) growth bands, but the bomb signal was weak, never exceeding a Δ^{14}C of −50. Similarly, Tauber (1979) reported some prebomb radiocarbon values based on marine mammal bones, but no chronology. A bomb chronology based on growth bands in beluga whales was much clearer, but the discovery that the teeth incorporated metabolic carbon rather than DIC suggested that mammalian chronologies in general would be expected to reflect their diet rather than the water in which they lived (Stewart et al. 2006).

Despite the unique environment of the Arctic, the 1957–1959 appearance of the bomb signal in the Arctic surface and deepwater marine radiocarbon chronologies was very similar to that of the reference chronology from the NWA, Northeast Pacific, and tropical regions around the world. The NWA chronology reported here represents an extension to that initially reported by Campana (1997), which was previously shown to have a virtually identical year of initial bomb radiocarbon increase to NWA chronologies based on bivalves (Weidman and Jones 1993) and corals (Druffel and Linick 1978). Otolith reference chronologies from the Northeast Pacific based on yelloweye rockfish (*Sebastes ruberrimus*) (Kerr et al. 2004) and Pacific halibut (*Hippoglossus stenolepis*) (Piner and Wischniowski 2004), an NWA chronology based on Atlantic cod (*G. morhua*) (Kalish et al. 2001), and a South Pacific chronology based on *Pagrus auratus* (Kalish 1993) all reported the initial appearance of bomb radiocarbon between 1957 and 1960, consistent with reports based on corals in the Central and South Pacific (Toggweiler et al. 1991; Guilderson and Schrag 1998). Clearly the appearance of the bomb signal is expected to be nearly synchronous in surface marine waters around the world, including the Arctic. An Antarctic reference chronology remains to be developed, but Peck and Brey (1996) reported the presence of a bomb signal in an Antarctic bivalve.

The close correspondence of otolith section age and the age indicated by the radiocarbon content of the adult otolith core indicates that our age estimates are realistic and validates our age interpretation criteria for lake trout. These results demonstrate that lake trout is a very long-lived species — at least 50 years — in the Arctic. Otolith transverse sections are now routinely applied to determine the age of many fishes, but such was not the case as recently as 20 years ago (Beamish and McFarlane 1987). With the realization that surface readings of otoliths often led to severe age underestimation in long-lived fishes (Beamish 1979), modern ageing methods often strive to prepare transverse sections or their functional equivalent, charred otolith halves. This development in ageing methodology explains why some early reports of lake trout growth and longevity appear to underestimate actual age (Johnson 1976). Power's (1978) insightful examination of otoliths broken through the core resulted in much greater ages, which were presumably more in keeping with the age interpretations reported here. However, the extremely narrow growth increments noted in the current study may indicate that even Power's (1978) age estimates were artifactually truncated at around age 45–50 years. We are not aware of any other published studies reporting annual otolith growth increments as narrow as 20 μm and thus below the resolution limit of a typical dissecting microscope. However, there are some reports of apparently "missing" annual increments in fish of known age (Beamish and McFarlane 2000; Dwyer et al. 2003). Conceivably, inadequate resolution could limit age determination accuracy in fish species where otolith growth is very slow.

The implications of having radiocarbon chronologies in the Arctic extend not only to ocean mixing models, but also to age determinations of Arctic organisms. Our age validation focused on lake trout in Arctic lakes, but the reference chronologies provided are applicable to the age validation of many terrestrial, freshwater, and marine organisms, as long as they contain calcified hard parts. Clearly, however, the difference in onset timing of the bomb signal between the freshwater and marine systems highlights the need to apply a reference chronology from a comparable environment to the animal being aged; for example, if the marine chronology was used to validate the age interpretation of a freshwater organism, an age underestimate on the order of 3–4 years could be expected, because of the earlier onset of the freshwater bomb signal.

With these new radiocarbon reference chronologies, age validation of a large number of Arctic organisms, both marine and freshwater, should now be possible. The age validation of Greenland halibut (Treble et al. 2008) and beluga whale (Stewart et al. 2006) has already been completed. Obvious candidates for future work include whitefish (*Coregonus* spp.) in Arctic lakes and Greenland cod, Arctic cod (*Boreogadus saida*), and bivalves in Arctic and subArctic oceans. As was the case with belugas, age validations need not be limited to fish or bivalves, suggesting that walruses, seals, and polar bears (*Ursus maritimus*) may also possess the bomb radiocarbon dated marker in their teeth. Such work will be critical to determine if slow growth and extended longevity are ubiquitous characteristics of Arctic organisms.

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Environmental enrichment in steelhead (*Oncorhynchus mykiss*) hatcheries: field evaluation of aggression, foraging, and territoriality in natural and hatchery fry

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Abstract: Reforms for salmonid hatcheries include production of hatchery fish with behavioral characteristics similar to wild conspecifics. Enrichment of the hatchery environment has been proposed to achieve this goal. Field experiments of steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) fry from a common stock reared under natural (i.e., stream), enriched hatchery, and conventional hatchery conditions indicated no significant differences in the rates of foraging or aggression between rearing treatments. However, the rates of foraging and aggression of natural fry were significantly affected by the type of hatchery fry stocked with them. Natural steelhead fry fed at lower rates and exhibited higher rates of aggression when stocked with steelhead fry raised in enriched hatchery environments. Territory sizes of steelhead fry ranged from 0.015 to 0.801 m^2; were significantly, positively related to body length; and were not significantly different between rearing treatments. We conclude that hatchery steelhead fry released into streams establish territories that are proportional to their body length and similar in size to territories of natural steelhead fry. Our results indicate that both conventional and enriched hatchery environments produce natural social behaviors in steelhead released as fry and that fry from enriched hatchery environments may alter the foraging and aggressive behavior of natural, resident steelhead fry.

Résumé : La production de poissons de pisciculture possédant des caractéristiques comportementales semblables à celles poissons sauvages de même espèce fait partie des réformes proposées pour l'élevage des salmonidés en pisciculture. On a suggéré d'enrichir l'environnement des piscicultures pour atteindre cet objectif. Des expériences de terrain avec des alevins de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) provenant d'un même stock, mais élevés dans des conditions de milieu naturel (c.-à-d., le cours d'eau), de pisciculture enrichie ou de pisciculture ordinaire, indiquent qu'il n'y a pas de différence significative dans les taux de recherche de nourriture et d'agression entre les groupes expérimentaux. Cependant, les taux de recherche et d'agression des alevins sauvages sont affectés significativement par le type d'alevins de pisciculture introduits avec eux. Des alevins de truites arc-en-ciel anadromes sauvages se nourrissent à des fréquences plus basses et montrent des taux plus élevés d'agression lorsqu'ils se retrouvent avec des alevins de truites arc-en-ciel anadromes élevés dans des environnements enrichis de pisciculture. La taille des territoires des alevins de truites arc-en-ciel anadromes varient de 0,015 à 0,801 m^2, ils sont reliés positivement à la longueur du corps et ils ne diffèrent pas significativement en fonction des diverses conditions d'élevage. Nous en concluons que les alevins de truites arc-en-ciel anadromes de pisciculture libérés dans les cours d'eau établissent des territoires qui sont proportionnels à la longueur de leur corps et semblables en taille à ceux des alevins des truites arc-en-ciel anadromes sauvages. Nos résultats indiquent que les environnements de piscicultures ordinaires et enrichies produisent des comportements sociaux naturels chez les truites arc-en-ciel anadromes utilisées pour les empoissonnements au stade d'alevin et que les alevins provenant des environnements de pisciculture enrichis peuvent altérer les comportement de recherche de nourriture et d'agression chez les alevins des truites arc-en-ciel résidantes sauvages.

[Traduit par la Rédaction]

Introduction

Several reviews have noted deficiencies in hatchery-based supplementation programs for salmonids, noting that hatchery-produced fish behave inferiorly in comparison with wild fish (Brown and Day 2002; Independent Scientific Advisory Board 2003; Huntingford 2004) and that stocked hatchery fish can displace or compete with wild fish (Einum

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and Fleming 2001). The majority of the hatchery stocks considered in the reviews had been raised using traditional hatchery protocols, and most evaluations of behavioral differences between hatchery and wild fish were conducted in the laboratory. In most cases, the behavioral differences between wild and hatchery stocks were attributed to the hatchery rearing environment (Einum and Fleming 2001; Huntingford 2004).

Common garden experiments, where salmonids of wild origin are raised under the same conditions as the hatchery strain, have provided evidence of behavioral divergence between hatchery and wild populations that may have a genetic basis. Differences between hatchery and wild juvenile salmonids in feeding, agonistic, and antipredator behaviors attributed to genetic divergence have been well documented (see reviews by Einum and Fleming 2001; Weber and Fausch 2003; Huntingford 2004). Factors causing genetic divergence affecting behavioral traits in hatchery populations include use of nonlocal broodstocks, unintentional and intentional selection in the hatchery, genetic drift, and inbreeding.

Most previously studied hatchery populations were not managed using a conservation hatchery approach. Modern conservation hatchery practices for anadromous salmonids include producing hatchery fish with behavioral characteristics of wild conspecifics, using locally derived broodstocks, integrating wild and hatchery populations to avoid genetic divergence, reducing artificial selection and inbreeding, and considering carrying capacity when calculating hatchery production (Flagg and Nash 1999). If conservation hatchery practices are followed, the behavioral differences between hatchery and wild populations attributed to genetic divergence are likely to be greatly reduced. In this case, the developmental effects of the hatchery environment on fish behavior become the primary concern. There are two relevant questions: (*i*) Do hatchery fish, because of the way they are reared, negatively impact wild fish after release? (*ii*) Can any negative effects on wild fish be lessened through manipulating the hatchery environment or employing alternative release strategies? Manipulations of the hatchery environment proposed to improve behavior and survival include overhead cover, underwater structure, underwater feed delivery, natural (gravel) substrate, and reduced hatchery residence time (Maynard et al. 1995; Flagg and Nash 1999; Brown and Day 2002).

Typically, steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) hatcheries produce yearling smolts that are presumed to migrate rapidly from freshwater streams to the ocean upon release. The duration of hatchery residence and its influence on behavioral development could be further reduced by releasing hatchery steelhead as fry. However, fry releases pose risks such as increased levels of interaction between hatchery and wild fry because of lengthened stream residence by hatchery fry. The benefits and risks of fry release might balance if fry releases produce hatchery fish that behave and use stream habitat in a similar manner as wild fish and if the total density of hatchery and wild fry does not exceed the stream carrying capacity. If carrying capacity were not exceeded, ecological interactions between hatchery and wild fish would be minimized by natural mechanisms and behaviors expressed by juvenile salmonids, such as the establishment and maintenance of individual territories.

Results of laboratory experiments suggest that enrichment of the hatchery environment can influence the agonistic behavior of hatchery-raised salmonids (Berejikian et al. 2001) and how they interact with natural conspecifics (Riley et al. 2005). Steelhead fry reared in a stream and in an enriched hatchery environment achieved higher social dominance rankings and had higher frequencies of threat displays than fry reared in conventional hatchery tanks (Berejikian et al. 2001). In a separate study (Riley et al. 2005), threat display frequency in steelhead fry was affected by stocking combination and stocking density. However, stocking combination had no effect on attack or feeding rates (Riley et al. 2005). Despite these laboratory findings, it has not been fully tested whether behavioral differences attributed to hatchery enrichment persist in natural streams or how fish raised in enriched hatchery environments interact in the wild with conspecifics.

We conducted research to determine if two different hatchery environments affected the behavioral development of steelhead released as fry in streams. As in the previously mentioned studies, half of the steelhead fry were produced using conventional hatchery conditions (hereafter referred to as conventional), while the other half were produced in an enriched hatchery environment (hereafter enriched) featuring overhead and underwater cover and underwater food delivery. We compared the enriched and conventional fry with steelhead fry raised in streams (hereafter natural). The conventional and enriched hatchery fry were obtained from the Skookumchuck River, Washington, and had the same genetic background as the natural fish used in this study; therefore, any differences observed between hatchery and natural steelhead could be attributed to rearing environment. Three response variables were measured: (*i*) foraging rate, (*ii*) aggression rate, and (*iii*) territory size. We chose these response variables because they have been previously measured in comparisons of hatchery and wild steelhead and thus provide a benchmark for comparing the performance of steelhead from conventional and enriched hatchery environments and how they affect natural fry. We tested three hypotheses: (1) Is natural fry behavior differentially affected by the type of hatchery fry (conventional or enriched) stocked into the enclosure with them? (2) Is the behavior of conventional and enriched hatchery fry comparable to natural fry behavior? (3) Do conventional and enriched hatchery fish exhibit similar behavior patterns?

Materials and methods

Rearing treatments

Steelhead eggs obtained from artificially spawned steelhead from the Skookumchuck River were incubated at the Washington Department of Fish and Wildlife's Bingham Creek Hatchery to the eyed egg stage in spring 2003. Eyed embryos were transported to the University of Washington's Big Beef Creek Research Station (Kitsap County, Washington) for final incubation in 10 °C well water.

After emergence, 2500 fry were stocked into each of six 1.8 m diameter circular indoor tanks near the end of May. Half of the tanks were conventional tanks that contained no cover or structure other than a standpipe. The other tanks were enriched and contained the tops of two fir trees, two 34 cm × 48 cm × 15 cm wire shopping baskets filled with cobbles, camouflage netting on top, and an underwater food-delivery system, which distributed commercial food pellets from automatic feeders through two 2.5 cm diameter nylon tubes near midwater depth (four food outlets per tank). Fish in the conventional tanks were fed by automatic feeders, which scattered the pellets across the water surface. All tanks received a constant flow of 40 $L \cdot min^{-1}$ of well water. Fluorescent lights controlled by a timer mimicked the natural photoperiod.

Study site

The experiment was conducted in Eleven and Twelve creeks, two second-order tributaries of the upper Skookumchuck River in the Chehalis River drainage in southwestern Washington. Fish passage to the upper Skookumchuck River is blocked by Skookumchuck Dam, but Washington Department of Fish and Wildlife and the dam owner (PacifiCorp) annually transport several hundred adult steelhead above the reservoir each spring to spawn naturally. Eleven and Twelve creeks are dominated by cobble and gravel substrate and drain second-growth riparian forest. In addition to steelhead, coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and sculpins (*Cottus* spp.) are present in Eleven and Twelve creeks.

Egg stocking

Snorkeling surveys and electrofishing conducted in 2002 indicated that natural production of steelhead fry in Eleven and Twelve creeks was low. To collect sufficient numbers of natural steelhead, we stocked eyed embryos obtained from the Bingham Creek hatchery (as above). One thousand eyed eggs were loaded into each of 25 Scotty salmonid egg incubators (Scott Plastics, British Columbia, Canada) on 9 April 2003 at the Big Beef Creek facility, held overnight submerged in well water, and transported the next day to Eleven and Twelve creeks. Thirteen units (containing 13 000 eyed eggs) were placed in Eleven Creek and 12 units (12 000 eyed eggs) were placed in Twelve Creek following the manufacturer's instructions. A correctly installed Scotty incubator allows fry to emerge from the incubator to take refuge in the gravel until the yolk sac is absorbed and feeding commences. Incubators were inspected weekly until fry were observed to ensure that the incubators remained submerged and covered with gravel.

Enclosures

We observed steelhead fry behavior within six enclosures that were constructed in each creek; all enclosures were located within 1 km from the mouth of each creek. Within a creek, the enclosures were consecutively numbered one through six, with enclosure number one occupying the most downstream position. Enclosures were constructed by placing stream-spanning weirs perpendicular to the stream flow. Weirs were constructed of modular panels (0.6 m × 1.5 m) framed with 1.9 cm polyvinyl chloride (PVC) pipe covered with 6 mm galvanized wire mesh. Panels were anchored with bailing wire to 1.2 m lengths of 1.6 cm rebar driven into the stream banks and substrate. Additional 6 mm wire mesh was attached over the seams between panels, and each panel had two plastic mesh skirts that were buried in the substrate and (or) covered with sand bags to prevent fish passage beneath the weirs. Enclosures varied in size from 90 to 215 m^2 (mean = 157 m^2) because of physical properties of the streams and limitations on where effective weirs could be constructed. All enclosures included both pool and riffle habitat, but the proportion of riffle and pool habitat varied among enclosures (Table 1). The total enclosure areas constructed in Eleven and Twelve creeks were 926 and 953 m^2, respectively.

Fish stocking

We attempted to remove all fry from the enclosures on 30–31 July 2003 by electrofishing each enclosure three times. Fry captured within the enclosures were saved and additional natural fry were collected from the tributaries and main channels of Eleven and Twelve creeks by electrofishing on 30–31 July 2003. Natural fry were stocked in each enclosure at a density of 0.27 $fry \cdot m^{-2}$ on 31 July 2003. Hatchery fry were transported to Eleven and Twelve creeks from the Big Beef facility and released on 31 July 2003. Either enriched or conventional hatchery fry were stocked into each enclosure at a density of 2 hatchery $fry \cdot m^{-2}$, mimicking hatchery-biased ratios seen in stocking programs. Thus, the total fry density in each enclosure was 2.27 $fry \cdot m^{-2}$ at the beginning of the study. Enriched hatchery fry were stocked into sections 1, 3, and 5 in Eleven Creek and sections 2, 4, and 6 in Twelve Creek; conventional fry were stocked into the remaining study sections in each creek. All fish were released at the midpoint of each study section. All hatchery-reared fish were double-marked with adipose and pelvic fin clips. The conventional fry had the right pelvic fin removed, and the enriched fry had the left pelvic fin removed. The combination of fin clips allowed us to discriminate between hatchery and natural fry and between enriched hatchery fry and conventional hatchery fry in the event that they escaped from the enclosures.

Behavioral observations

Underwater focal animal observations (Altman 1974) of steelhead fry were made by several observers while snorkeling in Eleven and Twelve creeks. Observers entered each enclosure from the downstream direction and randomly selected fish that appeared to be holding territories for observation. Within each enclosure, two wild fish and four hatchery fish were observed. When a fish was identified for observation, observers drew a map of the streambed on a plastic slate featuring four distinct landmarks (e.g., large distinct rocks or woody debris), noted the fish's focal point, and drew the location of all foraging strikes and aggressive acts on the map. Aggressive acts included frontal and lateral threat displays, charging, chasing, and nipping. Each fish was observed for 6 min. Observers also counted the number of conspecifics (hatchery or wild) within 1 m^2 around the focal point. After each observation period was complete, the observer estimated the fish's fork length and measured the actual distances between four pairs of landmarks on the map to calibrate the scale of the map. The distances between landmarks that were recorded by observers were used to scale the stream bottom map and estimate distances for each foraging and aggressive act. The actual distances between landmarks recorded by observers were measured on the slate, and the actual distance was divided by the measured distance; a correction factor was estimated as the mean of

Table 1. Properties and environmental characteristics of experimental enclosures on Eleven and Twelve creeks.

Enclosure No.	Length (m)	Mean width (m)	Area (m^2)	Pool habitat (%)	Riffle habitat (%)	SS (%)	G (%)	C (%)	Bo (%)	Br (%)
Eleven Creek (discharge = 0.089 $m^3 \cdot s^{-1}$)										
1	27.5	6.3	175	32.6	67.4	3.3	40.0	40.0	16.7	0.0
2	34.1	4.9	157	53.5	46.5	5.4	29.3	34.0	10.0	21.4
3	38.5	5.7	215	46.5	53.5	4.7	30.7	40.7	10.0	14.0
4	22.1	4.0	90	55.6	44.4	7.2	22.8	33.9	10.0	26.1
5	33.6	4.9	168	55.4	44.6	16.1	34.5	34.5	12.2	2.8
6	34.3	3.6	122	52.5	47.5	2.6	22.9	30.0	24.8	19.8
Twelve Creek (discharge = 0.082 $m^3 \cdot s^{-1}$)										
1	30.6	5.3	170	28.2	71.8	2.8	37.2	47.2	7.2	5.6
2	31	4.7	139	56.8	43.2	15.7	25.7	30.0	10.0	18.6
3	35.4	4.8	175	17.7	82.3	1.8	28.2	56.5	11.8	1.8
4	27.7	4.4	121	54.5	45.5	10.9	14.6	39.1	25.5	10.0
5	27.6	5.1	148	39.2	60.8	3.9	20.0	33.9	3.9	38.2
6	31.7	6.2	200	25.5	74.5	5.1	40.0	38.6	10.0	6.3

Note: SS, silt–sand; G, gravel; C, cobble; Bo, boulder; Br, bedrock.

the four quotients. The distance to the location of each foraging or aggressive act was then measured on the slate and multiplied by the correction factor to estimate the actual distance.

Behavioral observations were collected on eight occasions between 6 August and 11 September 2003 (6–7 August, 14–15 August, 27–28 August, and 9–11 September; pairs of dates were pooled for analysis and referred to as weeks 1 through 4, respectively). All observations were conducted between 1000 and 1500, and no counts were impeded by poor underwater visibility. Stream temperature ranged from 9.0 to 14.7 °C in Eleven Creek and from 8.7 to 14.1 °C in Twelve Creek during observations.

Data analysis

Rates of foraging and aggression were analyzed using unbalanced three-way analysis of variance (ANOVA), with stream, observation week, and rearing treatment (conventional, enriched, or natural) or fish type (hatchery or natural) as experimental factors. In this study, individual fish were the units of replication, and enclosures were simply used to separate stocking combinations, standardize stocking density, block by stream, and ensure representation of pool and riffle habitat in each enclosure. Data were analyzed using the general linear model procedure in MINITAB 14 (Minitab Inc. 2003). A subset of the foraging and aggression data were used in our analysis of territory size to ensure that only territorial steelhead fry were represented in our data set. Territorial steelhead (n = 136) were defined as those that displayed at least three aggressive acts. Fish were pooled across observation week and across streams to obtain sufficient sample size. Because relatively few fish exhibited high rates of aggression (only 72 fish initiated five or more aggressive acts), foraging distances were also used to estimate territory size. For all fry that initiated at least three aggressive acts, territory size (m^2) was estimated as the square of the mean of all recorded distances (foraging and aggression) from the focal point multiplied by pi. The three hypotheses (as above) were tested with analysis of covariance (ANCOVA), with fork length as the covariate, using the general linear model procedure in MINITAB 14 (Minitab Inc. 2003).

We used regression analysis to test whether the variation in territory size, foraging rate, and aggression rate were further explained by the density of fish in an area 1 m^2 around the focal fish. A paired t test was conducted to see if the area defended was equal in size to the area used for foraging. The ratio of area defended to area used for foraging was calculated and analyzed using ANOVA, with rearing type (conventional, enriched, or natural) as the dependent variable to test for behavioral differences in territory use and defense. All statistical analyses were performed using MINITAB 14 (Minitab Inc. 2003).

Results

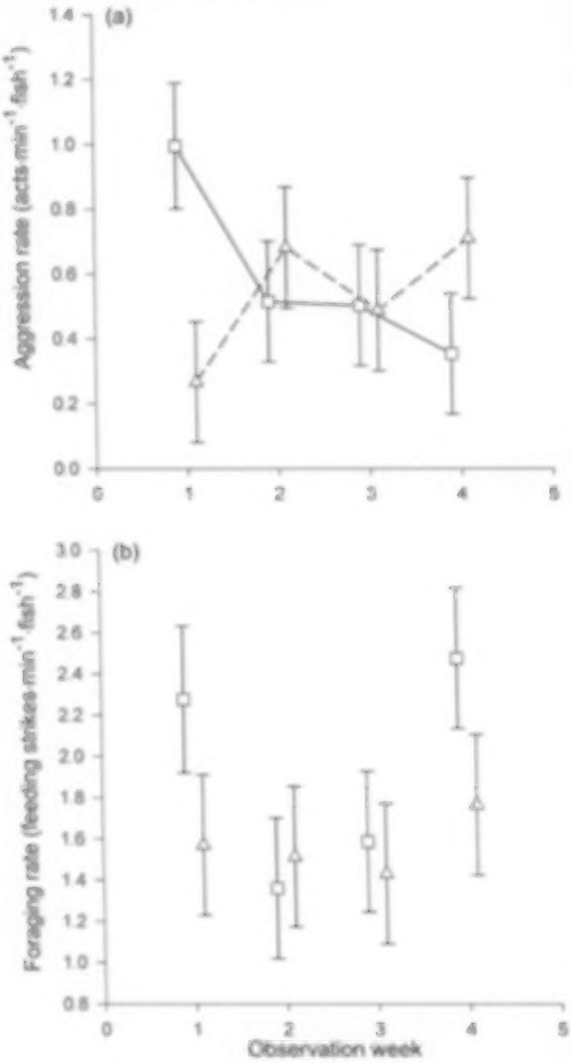
Effects of stocking conventional and enriched hatchery fry on natural fry

The rate of aggressive behavior of natural fry was affected by a significant interaction between observation week and the type of hatchery fry stocked with natural fry ($F_{[3,79]}$ = 3.97, p = 0.011). The aggression rate of natural fry in the presence of conventional hatchery fry generally decreased over the course of the experiment, but generally increased in the presence of enriched hatchery fry (Fig. 1a). The foraging rate of natural fry was significantly affected by type of hatchery fish stocked ($F_{[1,79]}$ = 5.01, p = 0.028) and by observation week ($F_{[3,79]}$ = 4.34, p = 0.007), but not by stream ($F_{[1,79]}$ = 0.65, p = 0.421). Foraging rates were lower for natural fry stocked with enriched hatchery fish than for natural fry stocked with conventional hatchery fish (Fig. 1b). The territory size of natural fry was not affected by the type of hatchery fry stocked ($F_{[1,45]}$ = 0.45, p = 0.504).

Comparison of conventional and enriched hatchery fry with natural fry

Because of the significant difference in foraging rate between natural fry stocked with the two hatchery types and the significant interaction between hatchery type stocked with natural fry and observation week affecting aggression rate, we

Fig. 1. (*a*) Average weekly aggression rates of natural steelhead fry (*Oncorhynchus mykiss*) stocked with conventional hatchery fry and natural fry stocked with enriched hatchery fry by observation week. (*b*) Average foraging rates of natural fry stocked with conventional hatchery fry and enriched hatchery fry by observation week. Natural fry stocked with conventional fry are represented by squares and solid lines, while natural fry stocked with enriched fry are represented by triangles and broken lines. Vertical bars are 95% confidence limits.



could not pool natural fry across hatchery stocking treatments. Therefore, comparisons of hatchery fry with natural fry were tested by comparing conventional hatchery fry and enriched hatchery fry with the natural fry present in their respective enclosures. The foraging rates of conventional ($F_{[1,127]}$ = 0.56, p = 0.455) and enriched hatchery fry ($F_{[1,128]}$ = 0.32, p = 0.574) were not significantly different than the natural fry stocked in their respective enclosures. The foraging rates of conventional and natural fry were significantly affected by observation week ($F_{[3,127]}$ = 4.43, p = 0.005; Figs. 2*a* and 2*b*). There was also a significant interaction between stream and observation week ($F_{[3,128]}$ = 5.01, p = 0.003; Figs. 2*a* and 2*b*) that affected the foraging rate of both enriched and natural fry.

The rates of aggression for conventional hatchery fry and natural fry were not significantly different ($F_{[1,127]}$ = 0.03, p = 0.871), but were significantly affected by observation week ($F_{[3,127]}$ = 4.34, p = 0.006). Rates of aggression decreased over time for conventional and natural fry. The rates of aggression for enriched hatchery fry and natural fry were affected by a significant interaction between observation week and fish type ($F_{[3,128]}$ = 4.12, p = 0.008). The aggression rate of natural fry increased with observation week, while the aggression rate for enriched hatchery fry decreased (Figs. 2*c* and 2*d*). Territory sizes of conventional fry and natural fry were not significantly different ($F_{[1,67]}$ = 0.05, p = 0.819) and neither were the territory sizes of enriched fry and natural fry ($F_{[1,63]}$ = 0.99, p = 0.324).

Comparison of conventional and enriched hatchery fry

There were no significant differences between conventional hatchery fry and enriched hatchery fry in foraging rate ($F_{[1,176]}$ = 1.85, p = 0.175), aggression rate ($F_{[1,176]}$ = 0.44, p = 0.508), or territory size ($F_{[1,87]}$ = 0.55, p = 0.460). The foraging rates of conventional and enriched hatchery fry were affected by a significant interaction between stream and observation week ($F_{[3,176]}$ = 4.56, p = 0.04). Observation week had a significant effect on the aggression rate of both hatchery types ($F_{[3,176]}$ = 5.94, p = 0.001), with the rate of aggression decreasing with observation week for both types of hatchery fry.

Territory size

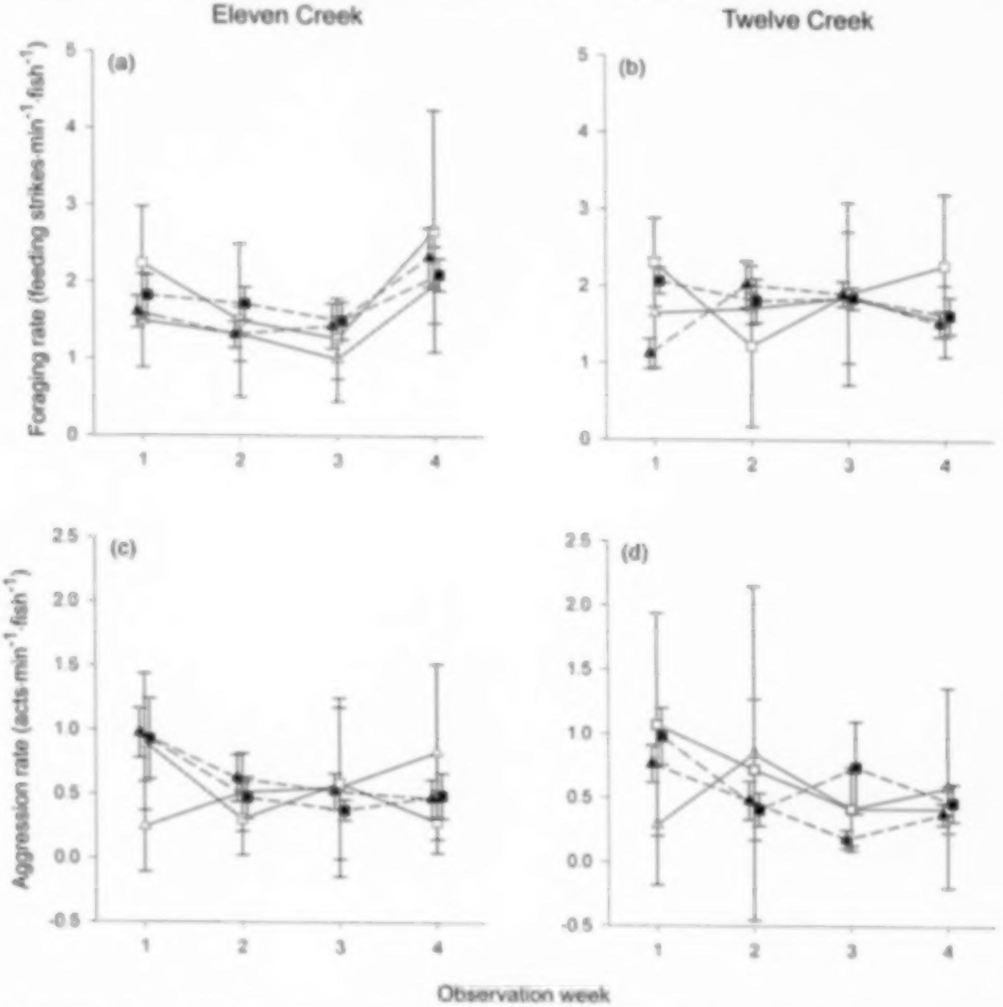
We found no significant differences in the territory sizes of conventional hatchery fry, enriched hatchery fry, and natural hatchery fry ($F_{[2,135]}$ = 0.043, p = 0.653), but the covariate, fork length, significantly affected territory size ($F_{[1,132]}$ = 9.40, p = 0.003). Territory size was related to body size by the equation $\log_{10}$(territory size) = 1.52 × $\log_{10}$(fork length) – 3.56 (Fig. 3). Territory sizes estimated in this study ranged from 0.015 to 0.801 m^2. Although the relationship between fork length and territory size was significant ($F_{[1,134]}$ = 11.67, p = 0.001, by linear regression), it explained a low proportion of the variability in territory size (r^2 = 0.08).

The area defended by aggressive behavior was significantly larger than the area used for foraging (n = 136, T value = 4.37, $p < 0.001$, paired t test). There was no significant difference among conventional, enriched, or natural fry in the ratio of the area defended to the area foraged, indicating similar spatial use of territories for all three types of steelhead fry ($F_{[2,133]}$ = 0.66, p = 0.520, one-way ANOVA). Territory size of steelhead fry was not affected by the local density (number of fry within 1 m^2 of the focal fish; p = 0.129, linear regression).

Discussion

Supplementation programs featuring conservation hatcheries for threatened and endangered anadromous salmonids as well as reform recommendations for conventional production hatcheries have both considered enrichment of the

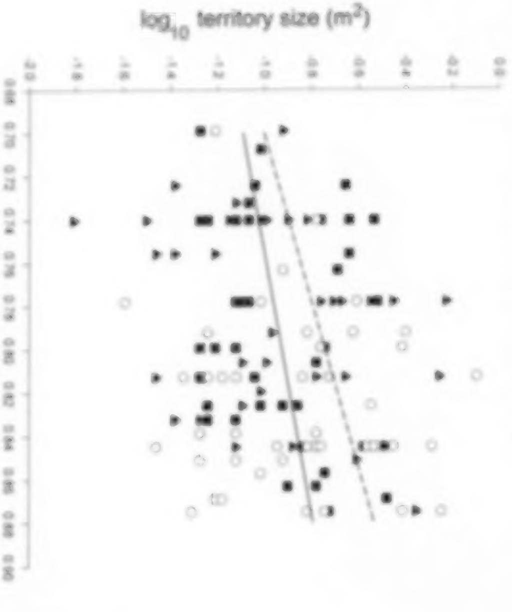
Fig. 2. Average foraging rates (panels *a* and *b*) and aggression rates (panels *c* and *d*) of steelhead fry (*Oncorhynchus mykiss*) in Eleven (panels *a* and *c*) and Twelve (panels *b* and *d*) creeks in summer 2003. Aggressive acts are the sum of threats and attacks. Natural fry stocked with enriched hatchery fry are represented by open triangles and solid lines; enriched hatchery fry are represented by solid triangles and broken lines; natural fry stocked with conventional fry are represented by open squares and solid lines; conventional hatchery fry are represented by solid squares and broken lines. Vertical bars are 95% confidence limits.



culture environment and alternative release strategies as methods to produce hatchery fish with characteristics of wild conspecifics. It is theorized that these culture and release practices will help to alleviate the risks and impacts to natural recipient populations when hatchery fish are stocked. Although many laboratory studies have demonstrated that environmental enrichment can change the behavior of hatchery-raised salmonids (Berejikian et al. 2000, 2001; Brown et al. 2003), there have been limited field evaluations of enrichment and fry releases (Riley et al. 2005). There is evidence that fish behavior observed under laboratory conditions may not reflect behavior in the wild (Sloman and Armstrong 2002; Sloman et al. 2002; Riley et al. 2005). This study evaluates how environmental enrichment affects the foraging, aggressive, and territorial behaviors of hatchery steelhead fry after release. It also evaluates the impacts of the two types of hatchery fish on the same behaviors in the recipient natural steelhead fry population.

We found that the foraging rates of steelhead fry observed in our study were similar to foraging rates reported in previous studies of similar-sized hatchery and wild steelhead fry observed under laboratory and stream conditions and at several densities (Keeley 2000; Imre et al. 2002; Riley et al. 2005). Foraging rates for steelhead fry in Eleven and Twelve creeks ranged from 0 to 5.5 strikes per minute per fish in our study (Table 2). Of most importance, we found that natural steelhead fry stocked with conventional fry had higher foraging rates than natural fry stocked with enriched fry. Because we observed no differences in the aggression rate, foraging rate, and territoriality between conventional and enriched fry, it is unlikely that these behaviors explain the reduced foraging rates of natural fry stocked with enriched fry.

Fig. 3. Territory size as a function of body length for all steelhead fry (*Oncorhynchus mykiss*) in Eleven and Twelve creeks. Natural fry are represented by open circles, conventional hatchery fry by solid squares, and enriched hatchery fry by solid triangles. The solid line represents the regression relationship for data from this study; the broken line represents the regression relationship reported by Grant and Kramer (1990).



Greater niche overlap between enriched and natural fry than between conventional and natural fry, or competitive differences (i.e., dominance) between conventional and enriched fry, might explain the difference in foraging rate of natural fry. The enriched hatchery fry were raised in tanks with underwater food delivery at the midpoint of the water column, while conventional fry were fed at the water surface. If enriched fry were accustomed to foraging within the water column like natural fry, there may have been greater competition between enriched and natural fry that reduced the foraging rate of natural fry. Additional support for this argument comes from previous behavioral studies that indicate steelhead fry raised in enriched environments perform more like natural fry than fry raised in conventional hatchery environments (Berejikian et al. 2000, 2001). In these studies, conventional hatchery steelhead fry were the least competitive. If the conventional hatchery steelhead fry in our study were less competitive and foraged higher in the water column than natural fry, then it is possible that competition for food between natural and conventional fry would be reduced, resulting in a higher foraging rate for natural fry. We did not measure foraging position in the water column; however, domesticated (hatchery) brook trout (*Salvelinus fontinalis*) have been observed to stay closer to the water surface than wild brook trout (Vincent 1960; Moyle 1969); and domesticated masu salmon (*Oncorhynchus masou*) foraged near the surface when offered slow-sinking pellets, while wild masu salmon initiated feeding bouts near the tank bottom (Reinhardt 2001).

Foraging rate may not accurately estimate foraging success (i.e., ingestion of a food item). We measured the total

Table 2. A comparison of aggression and foraging rates of steelhead fry (*Oncorhynchus mykiss*) observed in laboratory and stream settings.

Study	Setting	Rate range	Rate units	Mean fish length (cm) (SD)	Density (fry·m^{-2})
Aggression rates					
Present study	Stream (Skookumchuck River)	0–4	(Threats + attacks)·min^{-1}·fish^{-1}	6.4 (0.7)	2.27
Riley et al. 2005	Laboratory flume	0.2–3.5	(Threats + attacks)·min^{-1}·fish^{-1}	4.2–9.1 (size-matched)	1.8–7.1
	Stream (Skookumchuck River)	0.15–0.32	(Threats + attacks)·min^{-1}·fish^{-1}	Unknown	4–11
Imre et al. 2002	Laboratory stream channel	0.43–0.63	Interactions·min^{-1}·fish^{-1}	3.2 (0.03)*	23–27
Keeley 2000	Laboratory stream channel	0.57–2	(Chases + lateral displays)·min^{-1}·fish^{-1}	3.2 (0.1)	31.7–126.5
Keeley and McPhail 1998	Stream (Salmon River)	0.06–0.45	Intrusions·min^{-1}·fish^{-1}	7.2 (2.8)	1–7
	Stream (Chilliwack River)	0.08–0.67	Intrusions·min^{-1}·fish^{-1}	6.8 (4.9)	1–5
Slaney and Northcote 1974	Laboratory channel	0.5–1.1	Aggressive encounters·min^{-1}·fish^{-1}	3.1	108
Foraging rates					
Present study	Stream (Skookumchuck River)	0–5.5	Strikes·min^{-1}·fish^{-1}	6.4 (0.7)	2.3
Riley et al. 2005	Laboratory flume	0.2–0.4	Strikes·min^{-1}·fish^{-1}	4.2–9.1 (size-matched)	1.8–7.1
Riley et al. 2005	Stream (Skookumchuck River)	0.2–0.8	Strikes·min^{-1}·fish^{-1}	Unknown	2–12
Imre et al. 2002	Laboratory stream channel	6.2–6.8	Attempts·min^{-1}·fish^{-1}	3.2 (0.03)*	23–27
Keeley 2000	Laboratory stream channel	2.9–7.8	Strikes·min^{-1}·fish^{-1}	3.2 (0.1)	31.7–126.5

Note: SD, standard deviation.
*Standard error.

Table 3. Average territory size predicted by the regression relationship developed between fork length and territory size for several studies of juvenile steelhead (*Oncorhynchus mykiss*).

Study	Slope (β), intercept (α)	Average territory size (m^2)	Setting	Mean fish size (cm) (SD)	Fish density (fry·m^{-2})
Present study	1.68, –2.27	0.121	Stream	6.36 (0.67)	2.3 (total)
Imre et al. 2004	2.07, –2.91	0.057	Laboratory channel	2.59 (0.09)	24.8 (total), 37.2 (local)
Keeley and McPhail 1998	2.47, –2.74	0.179	Two streams	7.24 (2.82) and 6.83 (4.92)	2.9 and 2.7
Grant and Kramer 1990[a]	2.61, –2.83	0.189	Stream and laboratory	2.5 to 20	Unknown

Note: The fork lengths of juvenile steelhead in our study were used as the dependent variable in regression equations developed by previous authors; the average predicted territory size is reported. All slopes were not significantly different from the slope reported in our study (i.e., their slopes were within our 95% confidence limits; slope ± 95% confidence limits = 1.68 ± 1.02). SD, standard deviation.

[a] Regression equation reported in this study explains generalized relationship between territory size and fork length for five species of salmonids over a range of laboratory and field conditions obtained from previously published studies.

number of feeding strikes per minute per fish, and it is possible that some fry were striking at inappropriate objects in the drift (i.e., non-food items). Studies of natural juvenile brook trout in lakes (Biro et al. 1996) and streams (McLaughlin et al. 2000) found that capture rate and attack rate were poor predictors of ingestion rate. Juvenile brook trout in lakes ingested only 46% of captured prey items, while juvenile brook trout in streams ingested only 42% of attacked prey items. It is therefore possible that the lower foraging rates observed in natural fry stocked with enriched fry may not reflect significant differences in foraging success, especially if natural fry either discriminate better between food and nonfood items or have higher ingestion rates than hatchery fry. Significant differences in foraging success between wild and hatchery fish have been observed in the laboratory (Maynard et al. 1996; Ellis et al. 2002) and in streams after release (Munakata et al. 2000).

The rates of aggressive behavior of steelhead fry observed in our study were comparable to rates reported in previous studies of similar-sized hatchery and wild steelhead fry observed under laboratory and stream conditions and at several densities (Table 2). Rates of aggression were similar in both streams and ranged from 0 to 4 aggressive acts per minute per fish. Several laboratory studies have investigated the effects of enriched rearing environments on aggressive behavior using steelhead fry from the Skookumchuck River stock. Significant differences between rearing treatments in the rates of aggressive behaviors, primarily threat displays, were observed in several studies. One study documented significant differences in the rate of lateral displays between rearing treatments, with enriched fry being intermediate between natural and conventional fry, and both natural and enriched fry displaying significantly more than conventional fry (Berejikian et al. 2001). Another laboratory experiment found that rearing treatment combination and fish density affected the rate of threat displays (Riley et al. 2005). Yet another laboratory study (Riley et al. 2004*a*), conducted with the same enriched and conventional hatchery populations we used, found no differences in the threat or attack rates of natural fry stocked with conventional or enriched hatchery fry. None of the studies found significant differences in the attack rate between rearing treatments or between rearing treatment combinations. We measured aggression as the total number of attacks and threats initiated by the focal fish and did not distinguish whether an aggressive act was a threat or an attack during data collection. It is possible that fine-scale differences in aggressive behaviors between rearing treatments might be demonstrated if we were able to analyze threat rate and attack rate separately.

More holistic measures of aggression with proximate consequences (i.e., dominance) have also showed significant differences among conventional, enriched, and natural fry in two previous laboratory studies. Enriched hatchery steelhead fry socially dominated size-matched conventional hatchery fry (Berejikian et al. 2000). In a separate study, neither natural fry nor enriched hatchery fry dominated each other, but both dominated size-matched fry grown in conventional hatchery tanks (Berejikian et al. 2001). However, Riley et al. (2004*b*) found that fish density, but not hatchery rearing environment, played an important role in determining dominance. Beyond the factors of prior residence and large body size discrepancies between competing individuals (Rhodes and Quinn 1998), dominance is established through a combination of threat displays and attacks, so it is reasonable to consider dominance as a surrogate measure of overall aggression. Because of the similarities in dominance rankings of enriched and natural fry in two previous studies, it was thought that upon release, enriched hatchery fry might behave and integrate into the natural environment in a manner more similar to natural fish (Berejikian et al. 2001). If this were the case, in our study the aggressive behavior of the enriched hatchery fry should have increased with observation period, as did the natural fry. Therefore, it was surprising to find that only the natural fry exhibited increased aggression when stocked with enriched hatchery fry. We did not measure dominance in the field, and the equivocal results of previous laboratory studies (Berejikian et al. 2000, 2001; Riley et al. 2004*b*) make it difficult to assess whether hatchery rearing environment affects dominance of hatchery fish in streams. If enriched hatchery fish are superior competitors in comparison with conventional hatchery fish (Berejikian et al. 2000, 2001), then the increased aggression of natural fry in our study may be explained by more intense bouts of aggression during encounters between enriched and natural fry than between conventional fry and natural fry.

We found that rearing treatment had no significant effect on the size of territories established by juvenile steelhead fry in streams. Our results are in agreement with a previous laboratory study that reported no differences in space use among steelhead fry reared in natural, conventional, or enriched hatchery environments (Berejikian et al. 2001). Furthermore, the territory size of natural fry was not affected by the type of hatchery fry present. Because of the lack of significant differences between rearing treatments and stocking combinations, we pooled all territory size data for further analysis. The territory sizes of steelhead fry in our study increased with fork length, ranging from 0.015 to 0.801 m^2 and averaging 0.121 m^2, and were similar to territory sizes reported in previous studies of similar-sized hatchery and wild steelhead fry observed under laboratory and stream conditions and at several densities (Grant and Kramer 1990; Keeley and McPhail 1998; Imre et al. 2004; Table 3).

Juvenile steelhead defend territories from a centrally located station, from which they locate and expel intruding fish (Keeley and McPhail 1998). Foraging bouts are usually initiated from this same central station. Generally, the area defended is larger than the area used for foraging, but not always (Keeley 2000; Imre et al. 2004). Because all invertebrate drift that is available in a stream cannot be detected and eaten, steelhead fry may need to defend territories that are larger in size than would normally be required to meet their energetic demands (Keeley and McPhail 1998). The steelhead fry in our study aggressively defended areas larger than the area used for foraging, in agreement with these findings. Furthermore, there was no difference in the ratio of area defended to area foraged in for conventional, enriched, and natural fry, indicating similar spatial use of territories by all rearing treatments.

In contrast with previous studies, local density (number of fry within 1 m^2 of the focal fish) had no significant effect on territory size in our study. Three laboratory studies found that territory size of juvenile steelhead is inversely related to local population density (Keeley 2000; Imre et al. 2002, 2004). These studies used fish densities that are considerably higher than commonly observed in western Washington streams (Keeley 2000, 32–127 $fish \cdot m^{-2}$; Imre et al. 2002, 23–27 $fish \cdot m^{-2}$; Imre et al. 2004, 24.8 $fish \cdot m^{-2}$). However, Keeley and McPhail (1998) found an inverse relationship between density and territory size in streams where local densities ranged from 1 to 7 $fish \cdot m^{-2}$. The local densities in our study were similar to Keeley and McPhail (1998), averaging 5.6 $fish \cdot m^{-2}$ with a range of 1–22 $fish \cdot m^{-2}$.

In summary, our results indicate that there were few differences in aggressive behavior and foraging behavior among natural fry, conventional hatchery fry, and enriched hatchery fry when observed in streams. Furthermore, our results show that both enriched and conventional fry released into streams establish territories that are proportional to their body length, similar in size to and used in a fashion similar to territories established by natural steelhead fry. Our finding that rearing environment did not affect the rate of aggression tends to contrast with the results of laboratory studies of the same stock (Berejikian et al. 2000, 2001) that demonstrated rearing treatment affects specific aggressive behaviors (i.e., threat displays) and the establishment of dominance. However, the differences observed between rearing treatments in these laboratory studies offered potential explanations for the reduced foraging rate and increased aggression rate of natural fry in the presence of enriched hatchery fry. Most importantly, our results indicate that the behavior of natural resident fry differs depending on the type of hatchery fry stocked, with stockings of enriched fry producing increased aggression and decreased foraging relative to stockings of conventional fry. Laboratory assessments of the same hatchery populations we studied did not show differences in behavior when natural fry were stocked with conventional or enriched fry (Riley et al. 2004*a*). The discrepancy between the findings of the field and laboratory studies suggests that a complete evaluation of the effects of hatchery management reforms should include assessments of fish behavior and performance conducted under field conditions to identify effects that may not be fully documented in the laboratory.

The continued use of hatcheries as a tool to conserve and recover natural stocks has recently been evaluated, and a case has been made for hatchery reform (Hatchery Scientific Review Group 2004). Efforts to improve the contributions of hatchery-produced fish are now concentrated on the physiological, morphological, and behavioral traits of hatchery fish that may impart benefits when released. In these programs, wild fish may provide the best template for duplicating a quality hatchery fish (Hatchery Scientific Review Group 2004). Alterations to the hatchery environment, including enrichment, have been proposed as methods to achieve the wild fish template in the hatchery. Our results indicate that releases of fry grown in an enriched hatchery environment affect the feeding and agonistic behavior of the natural recipient population to a greater degree than releases of fry from a conventional hatchery environment, but it remains unknown whether simply increasing the density of natural fry would produce similar behavioral changes. Furthermore, the behavioral effects observed in this study may not occur in the more typical practice of releasing hatchery steelhead as yearling smolts. While our results indicate that releases of fry from enriched hatchery environments can affect the foraging and aggressive behaviors of natural fry, the magnitude of the consequences for long-term survival is unknown. More information about the survival, growth, adult return rate, and reproductive success of hatchery fish spawning naturally is needed to evaluate the effectiveness and the consequences of stocking hatchery fish that were reared in enriched hatchery environments.

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Increases in steelhead (*Oncorhynchus mykiss*) redd abundance resulting from two conservation hatchery strategies in the Hamma Hamma River, Washington

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Abstract: Conservation hatcheries for anadromous salmonids that aim to increase production and minimizing genetic, ecological, and demographic risks have not been experimentally tested for their ability to increase number of adults spawning in the natural environment. The conservation hatchery program for steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) evaluated in this study caused an increase in the number of redds in the supplemented Hamma Hamma River compared with the presupplementation period. Three control populations (nonsupplemented) either remained stable or declined over the same period. The increase in redds from hatchery-produced spawners did not reduce the redd production from natural-origin spawners. The strategy of rearing and releasing adult steelhead accounted for the greatest proportion of redd abundance increases. Environmentally induced differences in spawn timing between the adult release group and anadromous adults of hatchery and natural origin may explain why the adult release group and anadromous adults assortatively formed pairing combinations on the spawning grounds. Although captively reared adults produced the majority of redds in years they were released in substantial numbers, uncertainty regarding the relative reproductive success of this strategy suggests caution in recommending one strategy over the other. A demographic boost to the naturally spawning population was effected while managing to minimize negative ecological consequences.

Résumé : Les piscicultures de conservation de saumons anadromes cherchent à augmenter la production, tout en minimisant les risques génétiques, écologiques et démographiques; cependant, leur capacité à accroître le nombre d'adultes reproducteurs dans le milieu naturel n'a jamais été vérifiée expérimentalement. Le programme de pisciculture de conservation de la truite arc-en-ciel (*Oncorhynchus mykiss*) anadrome que nous évaluons a eu comme résultat d'augmenter le nombre de frayères dans la rivière Hamma Hamma après l'empoissonnement par rapport à la période antérieure. Trois populations témoins (sans empoissonnement) sont ou bien demeurées stables ou ont décliné pendant la même période. L'augmentation du nombre des frayères produites par les reproducteurs provenant de la pisciculture n'a pas réduit la production de frayères pour les poissons d'origine naturelle. La stratégie d'élevage et de libération de truites arc-en-ciel anadromes explique la plus grande partie de l'augmentation de l'abondance des frayères. Les différences dans le calendrier de la fraye induites par l'environnement entre le groupe d'adultes empoissonnés et les adultes anadromes d'origine naturelle ou de pisciculture peuvent expliquer pourquoi les adultes empoissonnés et les adultes anadromes s'assortissent en combinaisons de couples de même nature sur les milieux de fraye. Bien que les adultes élevés en captivité construisent la majorité des frayères les années où l'empoissonnement est important, l'incertitude entourant le succès reproductif relatif de cette stratégie incite à être prudent dans la recommandation d'une stratégie plutôt que de l'autre. Il s'est produit un accroissement de la population naturelle des reproducteurs, alors que les conséquences écologiques ont pu être minimisées.

[Traduit par la Rédaction]

Introduction

Artificial propagation of Pacific salmon (*Oncorhynchus* spp.) and steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) for conservation purposes is considered an experimental approach for maintaining or rebuilding depleted populations in the northwestern United States and Canada (ISAB 2003). The management objectives of conservation hatcheries vary, but most aim to prevent imminent biological extinction by amplifying the abundance of adult fish while at the same

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time maintaining the genetic integrity of the target population (Berejikian et al. 2004). Conservation hatchery programs collect embryos, juveniles, or adult broodstock from the wild and rear and release these same fish or their offspring into their natal or ancestral watersheds. Hatchery programs designed to supplement natural populations typically produce more spawners per artificially spawned parent than spawners produced per naturally spawning parent because of increased egg-to-smolt survival in the hatchery (ISAB 2003; Berejikian et al. 2004; Sharma et al. 2006). Conservation hatchery programs have yet to demonstrate that increases in adult returns lead to an increase in natural spawning in the composite (hatchery + natural) population.

Most published studies evaluating the effects of releasing hatchery-reared salmon or steelhead have concluded that the hatchery programs may reduce the survival or productivity of the natural populations (Levin et al. 2001; Nickelson 2003; but see Sharma et al. 2006). Studies published thus far have assessed the effects of large-scale hatchery programs operated to augment harvest or those utilizing non-native or highly domesticated hatchery broodstock. Analyses have relied on post hoc correlations (e.g., Levin et al. 2001; Chilcote 2003; Nickelson 2003) or modeling exercises (Oosterhout et al. 2005) rather than planned experiments. A true experimental approach requires reference populations that do not receive hatchery fish (Goodman 2004) and, ideally, a priori hypotheses tested with data from the presupplementation phase. Recent studies have compared the productivity of hatchery and natural coho salmon (*Oncorhynchus kisutch*) populations in a single watershed before and during supplementation (Sharma et al. 2006) and the relative reproductive success of hatchery and wild steelhead (Araki et al. 2006). However, neither study had the opportunity to include reference populations to account for factors such as spatial variability among watersheds or temporal variability in ocean productivity that may confound the evaluations of spawner abundance in supplemented streams (e.g., Hilborn and Winton 1993). The present study compares the number of steelhead redds before and during the implementation of a supplementation program and compares the response to three reference populations that were not supplemented to account for natural variability among populations.

Steelhead hatcheries throughout the Pacific Northwest almost invariably involve artificial spawning of adult broodstock and releasing age-1 smolts (natural-origin steelhead in Washington State typically undergo smoltification and migrate to sea at age-2; Busby et al. 1996). Artificial spawning, rearing, and release practices have been shown to advance spawn timing in conventional hatchery operations (steelhead: Ayerst 1977; McLean et al. 2005; coho salmon: Ford et al. 2006), reduce steelhead reproductive success (Leider et al. 1990; McLean et al. 2004), and alter juvenile steelhead behavior and predator-avoidance ability (Berejikian 1995; Berejikian et al. 1996). Hatchery programs operated for conservation purposes generally attempt to minimize genetic selection caused by artificial spawning and hatchery rearing, mimic the characteristics of natural fish, and scale the number of released smolts to the carrying capacity of the natural system (Flagg et al. 2004).

Conservation of several other anadromous salmonid populations listed as threatened or endangered under the US Endangered Species Act have recently been including nonconventional approaches to removing fish from the wild for culture and re-introducing them or their offspring. One such conservation hatchery program, the Hamma Hamma River Steelhead Supplementation Project, was initiated in 1998 with the goal of increasing the abundance of naturally spawning steelhead. This project included several nonconventional approaches aimed at minimizing potential negative impacts artificial propagation on the target natural population (no artificial spawning, natural age-at-smoltification, low numbers of released fish, and release of captively reared adults; see Materials and methods).

The goals of this evaluation were (*i*) compare changes in the abundance of redds produced in the Hamma Hamma River before and during the implementation of the hatchery program, (*ii*) estimate the contribution of captively reared adults to redd construction, and (*iii*) quantify spawn timing and breeding interactions between captively reared and anadromous spawners.

Materials and methods

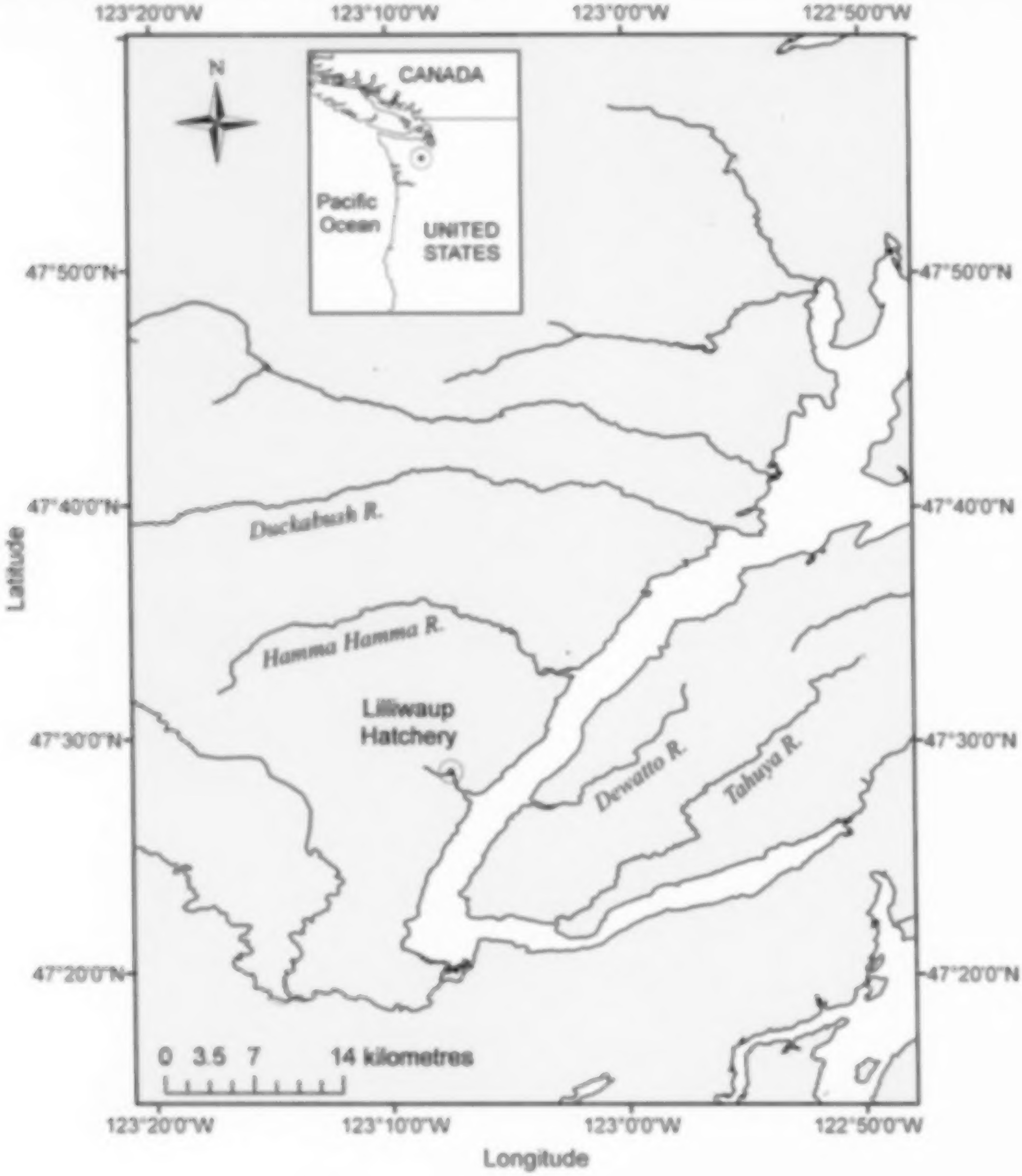
Study populations

The Hamma Hamma River drains the eastern slopes of the Olympic Mountains and flows into Hood Canal near the town of Eldon, Washington (Fig. 1). The Hamma Hamma watershed is about 137 km^2 in area, contains 29 km of mainstem and 150 km of tributary habitat, and has an average annual discharge of 16.1 $m^3 \cdot s^{-1}$. However, anadromous fish passage is limited to the lower 3.8 km, where a natural fall blocks upstream migration of adults. Habitat in the anadromous habitat below river km 3.8 contains a mix of forest land including old growth and second growth timber, pasture, and residential property, all of which is owned by the Hamma Hamma Timber Company.

The Hamma Hamma River wild steelhead sport angler harvest averaged 89 adults between 1950 and 1987. In the subsequent 3 years, reported sport angler harvest dropped to 11, 8, and 4 adults, respectively, and harvest of wild adults has been prohibited since 1990. Prior to supplementation effort initiated in 1998, the Hamma Hamma River received only a single outplanting of 5930 hatchery smolts in 1953. An unknown proportion of adult *O. mykiss* in the Hamma Hamma River exhibit a resident life history, do not migrate to sea, and mature in fresh water (see Kuligowski et al. 2005).

Three rivers in the Hood Canal Watershed contained nonsupplemented "control" populations, located on the west and east sides of Hood Canal and north and south of the Hamma Hamma River (Fig. 1). The Dewatto River watershed (48 km^2) contains 14 km of mainstem and has an average annual discharge of 2.16 $m^3 \cdot s^{-1}$. The Tahuya River contains 33.9 km of mainstem and has an annual average discharge of 4.3 $m^3 \cdot s^{-1}$. The Duckabush watershed (194 km^2) contains 40 km of mainstem and has an average annual discharge of 13.6 $m^3 \cdot s^{-1}$. Anadromous steelhead have access to the lower 10 km of the Duckabush River watershed, the lower 19 km of the Tahuya River watershed, and 10 km of the Dewatto River watershed, although a large wetland complex may limit adult steelhead migrations to the lower 5 km of the Dewatto River.

Fig. 1. Map of the Hood Canal watershed showing the supplemented river (Hamma Hamma), the three control rivers (Duckabush, Dewatto, and Tahuya), and the Lilliwaup hatchery in Washington, USA.


123°20'0"W
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123°0'0"W
122°50'0"W
N
CANADA
Pacific Ocean
UNITED STATES
47°50'0"N
47°40'0"N
47°30'0"N
47°20'0"N
Latitude
Duckabush R.
Hamma Hamma R.
Lilliwaup Hatchery
Dewatto R.
Tahuya R.
0 3.5 7 14 kilometres
Longitude

No smolts were released into the Dewatto or Tahuya rivers during the course of this study. Releases of hatchery-reared steelhead smolts into the Duckabush River from 1995 to 2002 (1997 to 2004 return years) have averaged (± standard deviation, SD) 8442 (±3598). The smolts released into the Duckabush River were derived from a Puget Sound population (Chambers Creek) that had been selected for substantially advanced spawn timing, with peak spawning occurring in December and January (Ayerst 1977). Thus, redds produced by hatchery females escaping to the spawning grounds would not have been counted in the redd surveys occurring when wild fish spawn (from late February through early June of each year). Similarly, McMillan et al. (2007) found no evidence over 5 years of spawning interactions between steelhead derived from the same hatchery stock and natural-origin steelhead in two western Washington streams.

The Hamma Hamma River hatchery population was established by hydraulic removal of eyed steelhead eggs (em-

Table 1. The number of eyed embryos collected, number of juveniles released at age-1 and age-2, and number of maturing adults released at age-4 and age-5.

			John Creek Pond		Lilliwaup Hatchery	Adult release group	
Brood year	Redds represented	Eggs collected	Age-1[b]	Age-2	Age-2	Age-4	Age-5
1998[a]	8	4683	1711	0	1524	81 F, 116 M	2 F, 2 M
1999	6	2588	466	435	901		
2000	7	1622	601	8	481	35 F, 41 M	10 F, 15 M
2001	4	2000	577	150	727		

Note: Adults from brood year 1998 were released in 2002 (age-4) and 2003 (age-5); adults from brood year 2000 were released in 2004 (age-4) and 2005 (age-5). F, female; M, male.

[a] The majority of smolts released from the 1998 brood year would be expected to spawn for the first time in 2002 at age-4.

[b] Age-1 fish "released" from the John Creek Pond represent escapees resulting from various temporary pond failures during the winter prior to their intended release. Escapes occurred in every year when the fish were approximately 16–18 months of age. Escaped fish entered John Creek and still may have contributed to adult returns (all were marked prior to escape).

bryos) in spring–summer of 1998–2001 using methodology similar to that described by Collins et al. (2000). Each year, the resulting fry were reared at two locations: (*i*) an earthen spring-fed pond located near John Creek, the main tributary of the Hamma Hamma River below the anadromous barrier, and (*ii*) circular rearing vessels at the Long Live the Kings Hatchery near Lilliwaup, Washington, approximately 10 km south of the Hamma Hamma River. Hereafter, fish reared and released at the smolt stage are referred to as the smolt release group (SRG), and fish reared and released at the adult stage are known as the adult release group (ARG). The ARG fish were reared only at the Lilliwaup Hatchery.

Age-2 smolts were released on 1 May each year beginning in 2000, and adults were released between 12 February and 6 March (depending on the year) to coincide with the onset of ovulation in females from the ARG population (Table 1). The fork length of ARG fish at the time of release averaged 525 mm in 2002, 633 mm in 2003, 502 mm in 2004, and 683 mm in 2005. The fork length of SRG fish at the time of release averaged 185 mm in 2000, 182 mm in 2001, 206 mm in 2002, and 178 mm in 2003. The SRG fish reared at the Lilliwaup Hatchery were marked by removal of the adipose fin and insertion of a coded-wire tag approximately 1 month prior to release. The SRG fish reared at the John Creek Pond had their adipose fin removed, but were not coded-wire-tagged. A uniquely numbered 3 cm long Floy anchor tag was inserted into the dorsal musculature of every released ARG fish (a different color was used each year).

Redd surveys

Redd surveys were conducted in the Hamma Hamma River and the three control rivers during each year of the study. The presupplementation period was represented by surveys conducted annually from 1997 through 2001, and the supplementation period included the years 2002–2006. Surveys were conducted by walking along the stream banks and in the streams. We used data from annual Washington Department of Fish and Wildlife (WDFW) redd surveys in all study streams. Redd survey frequency in the Hamma Hamma River increased beginning in 2002 to facilitate other data collection (e.g., reproductive behavior, marking redd locations for embryo collections, and capturing adult steelhead for genetic and age data). Survey frequencies were intentionally increased in the Duckabush River from 2003 through 2006 and in the Dewatto River from 2004 through 2006 to more closely match the increased survey frequency in the Hamma Hamma River during the supplementation period and to provide a basis for estimating the effect of survey frequency on redd abundance.

Redd surveys are a frequently used and widely accepted method for estimating adult salmon and steelhead abundance (Nickelson 2003; Gallagher and Gallagher 2005; Sharma et al. 2006). Crews of two walked the index reaches of each stream searching for redds. All redds were uniquely marked with labeled flagging, tied to vegetation on the stream bank. Redds were identified as described in previous studies (Gallagher and Gallagher 2005) by a clear "tail-spill" (usually crescent-shaped), resulting from material excavated to construct a nest pocket. Redds containing a minimum of 1 m of unexcavated gravel between them were considered separate. In cases where redds had remained the same size for at least 4 days and were later enlarged (or altered to account for superimposition), the enlarged area was counted as an additional redd. Berejikian et al. (2005) found that female steelhead spawned, on average, over a 4.0-day period, with females observed to be enlarging the redd each day from the onset to termination of spawning. In this study, we used the numbers of redds as the response variable for statistical tests to eliminate potential random error associated with redds-per-female and sex ratio estimates.

Spawning behavior and timing

The reproductive behavior of maturing steelhead in the Hamma Hamma River was monitored several days each week from the stream bank during the spawning season from 2002 to 2004 for three purposes: (*i*) test the null hypothesis that ARG and anadromous (SRG or wild) steelhead did not exhibit assortative mating as inferred from pairing combinations; (*ii*) test the null hypothesis that ARG and anadromous females did not differ in spawn timing; and (*iii*) obtain point estimates for the proportion of redds that were constructed by ARG and anadromous females in years where substantial numbers of each group were present (i.e., 2002 and 2004). Behavioral observation methods and data on just the pairing combinations in 2002 are presented in Berejikian et al. (2005). In both years, observers walked along both stream banks to locate nest-digging females and attempted to determine their rearing history based on the adipose fin marks and the presence or absence of an anchor tag. Unfortunately, observers could not reliably determine adipose fin presence and absence, so SRG and wild fish could not be distinguished from one another and were combined into an "anadromous" category. Observers determined the dominant or courting male within the hierarchy of males surrounding each nest-digging female. Courting males were those holding the position closest to a nest-digging female and exhibiting courtship behavior (quivers and crossovers). Courting males would also frequently chase off other peripheral males that held positions downstream and would frequently dart into the nest. Courting frequency has been shown to be a strong indicator of actual breeding success in this population of steelhead (Berejikian et al. 2005), which is generally confirmed by other studies of salmonids (e.g., Quinn and Foote 1994; Mjölnerod et al. 1998; Blanchfield et al. 2003). The number of different nesting females from each group and the frequency of each pairing combination (i.e., a nest-digging female and courting male) were tabulated for each year in which observations were made.

Spawner abundance

Counts of live adult steelhead were made by snorkel surveys to calculate the proportions of observed ARG, SRG, and wild adult steelhead present in the Hamma Hamma River during the supplementation period (2002–2006). Snorkel surveys were conducted approximately weekly from river km 3.0 downstream to the area of tidal influence (approximately river km 1.2) to count fish. Surveyors walked upstream along the entire study section before snorkeling to look for fish and count redds. Surveyors kept track of the number of redds visible while on foot (redds observed during snorkeling that were not observed in the preceding foot survey were recorded separately). Once at the upstream end the study section, surveyors floated downstream to look for fish. When a steelhead was spotted, surveyors attempted to identify the presence or absence of an adipose fin, anchor tag presence or absence and color, and body length. Surveyors categorized *O. mykiss* as either greater or less than 42 cm in length (surveyors previously practiced identifying the size of objects underwater by comparing them to objects of known length). The robust body condition and often silvery appearance of *O. mykiss* greater than 42 cm suggested that these fish were anadromous (i.e., steelhead). Analyses of scales from 12 *O. mykiss* collected from the Hamma Hamma River between 42 and 50 cm have shown that six were anadromous, two were nonanadromous, and the life history of the other four could not be determined because of scale regeneration (J. Sneva, WDFW, 600 Capitol Way North, Olympia, WA 98501, USA, personal communication, 2005). We calculated the average number of fish from each group per survey within each year to estimate the proportion of adult steelhead from the ARG, SRG, and wild groups. Ten surveys were conducted in 2002, 11 in 2003, 16 in 2004, 14 in 2005, and 13 in 2006.

Redd construction by ARG, SRG, and wild steelhead

We calculated point estimates for the relative contribution of the ARG, SRG, and wild steelhead to redd construction in the Hamma Hamma River using a behavior-based estimate (in 2002 and 2004) and an abundance-based estimate (all years from 2002 through 2006). For the behavior-based estimate, we calculated the proportion of ARG and anadromous females that were observed to be constructing redds in 2002 ($N = 24$) and 2004 ($N = 20$). Females observed digging a nest were considered to have constructed the redd at that location.

The abundance-based estimate assumed that per capita redd production would be the same for adults from each of the three groups present on spawning grounds, which is supported by the following. First, a portion (24 females and 24 males) of the ARG were released into an experimental spawning channel in 2002. The females deposited an average of 98% of their estimated fecundity, no females spawned fewer than two times, and 100% of the 24 females produced fry (as determined by DNA pedigree analysis, Berejikian et al. 2005). Second, the average number of redds constructed by ARG females (1.42 redds per female) in the spawning channel was similar to other estimates of redds per female for wild steelhead (1.6 redds per female by wild steelhead in the Hamma Hamma River, Kuligowski et al. 2005; 1.5 redds per female in the Nestucca River, Oregon, Susac and Jacobs 2001; and 1.2 redds per female in Snow Creek, Washington, Johnson and Cooper 1992). Third, 10 of 14 ARG females that were recaptured by hook and line in 2002 had deposited all of their eggs; the other four had eggs that could be easily expressed, but appeared viable (i.e., not overripe or water-hardened), indicating they still had the potential to deposit the eggs. In 2004, 10 of 14 females had deposited all of their eggs, two had not yet ovulated, and two were ovulated with apparently viable eggs (B.A. Berejikian, unpublished data).

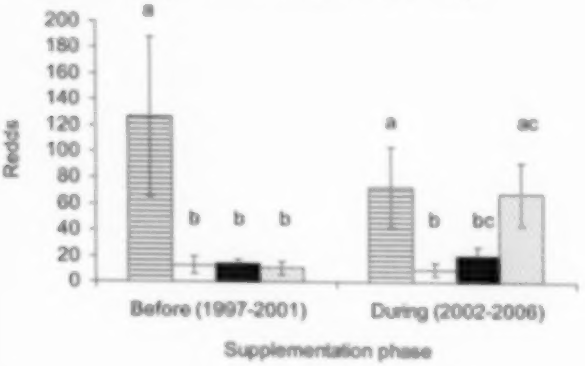
For the abundance-based estimate, we calculated the number of redds constructed by each group by multiplying the proportionate abundance of adults from each group observed during the snorkel surveys by the total number of redds observed in the same year. To evaluate concordance between the abundance- and behavior-based estimates, we compared the anadromous versus ARG behavior-based estimates in 2002 and 2004 with the anadromous versus ARG abundance-based estimates in those same years.

Statistical analyses

To assess whether the number of redds observed may have been influenced by survey frequency, redd survey frequency in a given year was regressed against the number of redds observed. Regressions for the Tahuya, Dewatto, and Duckabush rivers include all years (presupplementation and during supplementation). The Hamma Hamma River regressions were run separately for presupplementation and during supplementation periods because the substantial numbers of hatchery-reared fish observed constructing redds during the supplementation period would have confounded an analysis across the two periods.

In the absence of significant correlations between survey frequency and number of redds observed for any of the populations (see Results), redd abundance data were subjected to an analysis of variance (ANOVA), in which the main effects were period (before and during supplementation) and population (Dewatto, Duckabush, Tahuya, and Hamma Hamma). We tested the hypothesis that supplementation would have a different effect on redd abundance in the Hamma Hamma population than that in the other three populations. This effect

Fig. 2. The annual average number redds (±95% confidence intervals) in the supplemented river (Hamma Hamma, stippled bars) and the three control rivers (Tahuya, striped bars; Duckabush, open bars; and Dewatto, solid bars) before (1995–2001) and during (2002–2006) supplementation in the Hamma Hamma River. Different letters indicated significant differences as determined by Tukey's honestly significant difference tests ($\alpha = 0.05$).



would be reflected in a significant interaction between population and period. We conducted pairwise Tukey's honestly significant difference comparisons of cell means (e.g., Hamma Hamma River presupplementation versus Hamma Hamma River during supplementation) to identify changes in the relative abundance of redds in the Hamma Hamma River and the three control rivers.

We used the behavioral data to test the hypothesis that ARG and anadromous steelhead formed pairs without regard to whether their mates were ARG or anadromous; data were analyzed by χ^2 tests of independence (Sokal and Rolf 1995). The same nesting and courting data were used as surrogate measures of spawn timing. We tested for differences in spawn timing between ARG and anadromous males and females in 2002 and 2004 with a two-factor ANOVA (main effects: year and group; separate test for each gender). Significance level was $\alpha = 0.05$ for all statistical tests.

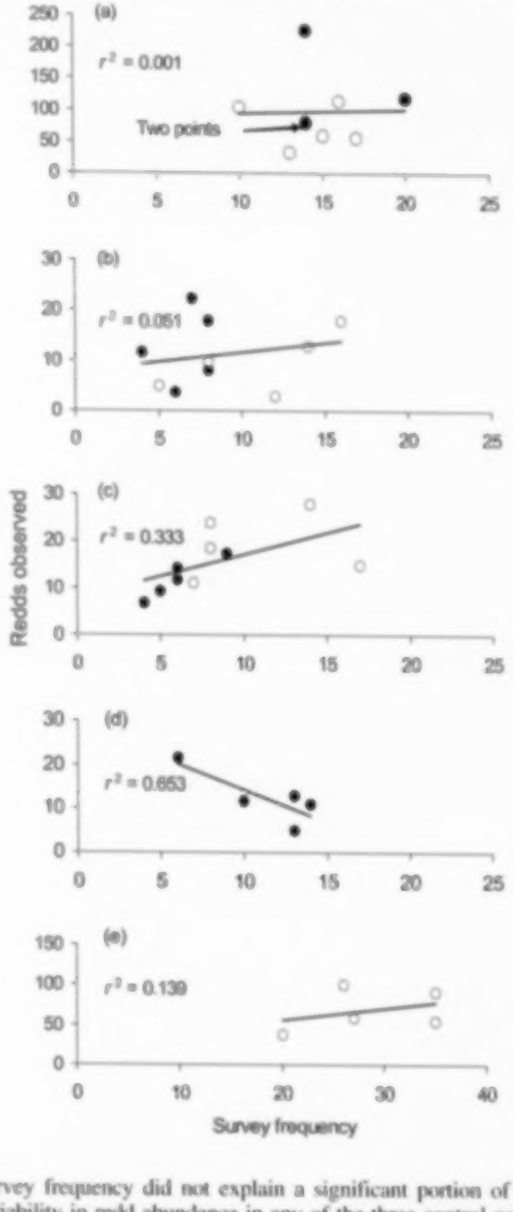
Results

Redd and spawner abundance

There was a significant interaction between the two main factors (supplementation phase and population) for the number of redds observed ($F_{(3,31)}$, $P = 0.001$; Fig. 2). The number of redds in the Hamma Hamma River during supplementation was significantly greater than that in the presupplementation period. In contrast, average redd abundance in the Dewatto and Duckabush populations was quite similar in the presupplementation and during supplementation periods, and the Tahuya population showed a decline (Fig. 2). No significant changes were detected between the before and after supplementation periods within the nonsupplemented rivers (e.g., Tahuya River before supplementation versus Tahuya River after supplementation; $P > 0.05$ for all comparisons, Fig. 2).

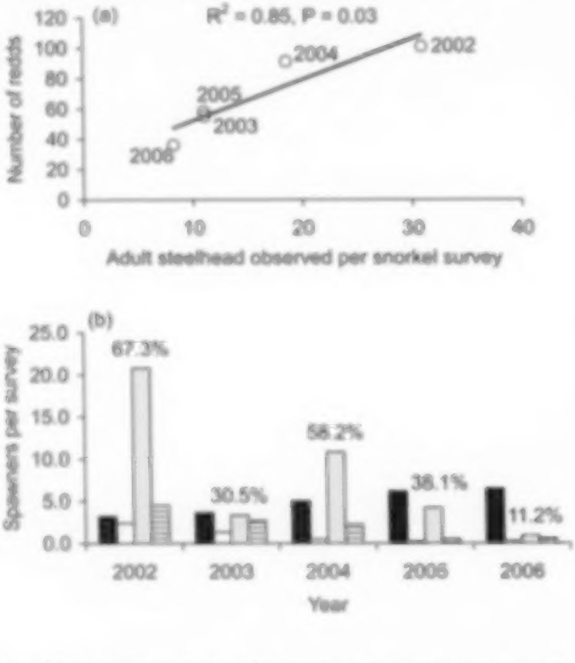
Redd survey frequencies in both the Hamma Hamma River and control rivers were greater during the supplementation period than during the presupplementation period; however, the increase was greatest in the Hamma Hamma River (Fig. 3).

Fig. 3. Simple linear regression analyses testing the correlations between the annual redd survey frequency and the number of redds observed in the three control rivers: Tahuya (*a*), Duckabush (*b*), and Dewatto (*c*). The presupplementation (solid circles) and during supplementation (open circles) years in Hamma Hamma River data (panels *d* and *e*) were analyzed separately to minimize confounding effects of adding hatchery fish, which were observed spawning. None of the correlations were significant ($\alpha = 0.05$).



Survey frequency did not explain a significant portion of the variability in redd abundance in any of the three control populations or the Hamma Hamma population (Fig. 3). The presupplementation period in the Hamma Hamma population showed the strongest correlation ($r^2 = 0.653$, $n = 5$, $P = 0.098$) between survey frequency and redd abundance; however, the slope was negative. The slopes of the linear regression rela-

Fig. 4. (*a*) The relationship between the annual number of redds observed and the annual average number of adult steelhead (*Oncorhynchus mykiss*) observed during the snorkel surveys from 2002 through 2006. (*b*) The average annual number of adult steelhead identified by group (wild, solid bars; smolt release group (SRG), open bars; adult release group (ARG), stippled bars; unknown origin, striped bars). The percentage of adults belonging to the ARG group is shown above each ARG bar.



tionships tended to be weakly positive in the Tahuya population ($r^2 = 0.001$, $n = 9$, $P > 0.50$) and Duckabush population ($r^2 = 0.051$, $n = 10$, $P > 0.50$); the slope was stronger in the Dewatto population, but still nonsignificant ($r^2 = 0.333$, $n = 10$, $P > 0.05$). These data suggest redd survey frequency differences among streams or between periods did not bias the analysis comparing redd abundance before and during supplementation in the four populations.

In the Hamma Hamma River, the number of redds observed was significantly and highly correlated with the average number of adult steelhead observed during snorkel surveys during the supplementation period (Fig. 4*a*). The proportion of adult steelhead from the three groups varied substantially among years and appeared to be largely a result of the numbers of ARG fish that were released in a given year (Table 1, Fig. 4*b*).

Spawning behavior and timing

We observed 24 courting pairs of steelhead in 2002 and 20 pairs in 2004. In 2002, 70% (17 of 24) of females observed constructing nests were from the ARG, and 30% were anadromous (SRG and wild combined). In 2004, 55% (11 of 20) of the nesting females were from the ARG, and 45% were anadromous. The χ^2 analysis indicated that the two groups paired assortatively when data from both years were combined ($\chi^2 = 10.91$, $P < 0.01$; Table 2). The results were similar when analyzing data from 2004 ($P < 0.01$) and 2002 ($P = 0.05$).

Table 2. The number of adult release group (ARG) and anadromous (combination of wild and returning hatchery-reared) male and female steelhead (*Oncorhynchus mykiss*) participating in courtships in the Hamma Hamma River in 2002 and 2004.

	ARG male	Anadromous male
2002		
ARG female	14	3
Anadromous female	3	4
2004		
ARG female	10	1
Anadromous female	3	6
Combined		
ARG female	24	4
Anadromous female	6	10

The assortative pairing was consistent with differences between the ARG and anadromous groups in the observed timing of spawning activity. Females from the ARG were observed nesting earlier than anadromous females in both years (group effect: $F_{[1,41]} = 14.96$, $P < 0.001$; year effect: $F_{[1,41]} = 2.22$, $P = 0.144$; group × year interaction: $F_{[1,41]} = 0.18$, $P = 0.673$; Fig. 5). Males from the ARG group were observed courting earlier than anadromous males (group effect: $F_{[1,41]} = 8.66$, $P = 0.005$; year effect: $F_{[1,41]} = 1.54$, $P = 0.222$; group × year interaction: $F_{[1,41]} = 0.811$, $P = 0.373$; Fig. 5).

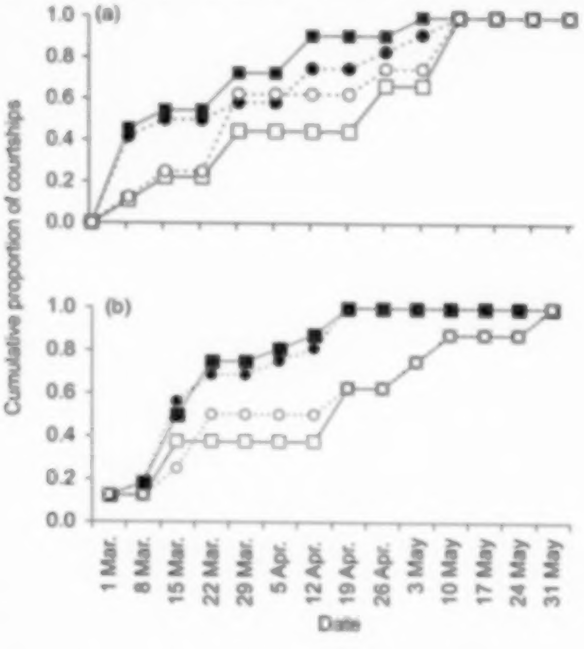
Redd construction by ARG, SRG, and wild steelhead

The behavior-based estimates of redd construction indicate that the ARG steelhead constructed 70% of the redds in 2002 and 55% of the redds in 2004. The abundance-based estimate of redd construction indicate that ARG steelhead constructed 67% and 58% of the redds in those two years, respectively (Fig. 4*b*, Fig. 6). Thus, there was strong concordance in the results using these two approaches. The abundance-based estimates for all supplementation years indicate that ARG females constructed the greatest number of redds in years when more were released and fewer in years when fewer were released; the fewest number of redds was constructed by the SRG group in all years (Table 1; Fig. 6). The lowest number of redds during the supplementation period was in 2006. The majority of adults observed were wild and may have represented age-5 offspring of wild steelhead spawning in 2001, age-4 offspring of hatchery or wild parents spawning in 2002 (age-4 offspring), or age-3 offspring of hatchery or wild parents spawning in 2003. Hatchery-produced spawners were expected to be at low abundance, because only age-5 and older SRG or age-6 repeat spawning ARG adults were present. Nevertheless, the number of redds in 2006 ($n = 39$) was approximately 3.5 times greater than the 5-year presupplementation average ($n = 11$; Fig. 6).

Discussion

The salient findings of this study are as follows: (*i*) the conservation hatchery program has caused an increase in the

Fig. 5. The cumulative frequency of adult release group (ARG) females (■), anadromous females (□), ARG males (●), and anadromous males (○) observed participating in courtships in the Hamma Hamma River in 2002 (*a*) and 2004 (*b*).

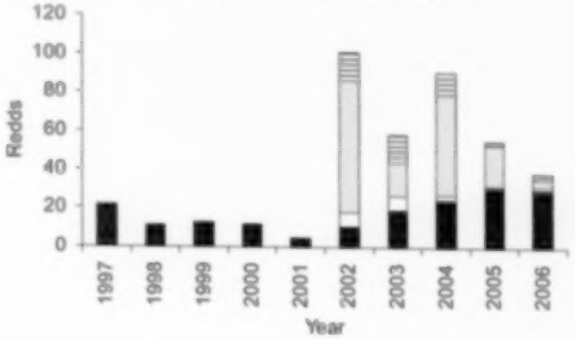


number of redds in the Hamma Hamma River without reducing the redd production from natural-origin spawners, (*ii*) the adult release strategy contributed the greatest proportion of the increase in years when substantial numbers of ARG steelhead were released, and (*iii*) differences in spawn timing probably explain the assortative pairing in the ARG and anadromous groups.

The findings of the present study add to other recent indications that supplementation programs may contribute to short-term increases in salmon and steelhead populations. A coho salmon supplementation project that brought wild spawners into the hatchery, spawned them, and released their offspring as smolts appears to have increased smolt production capacity, while the natural population productivity remained fairly stable (Sharma et al. 2006). Araki et al. (2006) extrapolated results of the relative reproductive success of hatchery-born and wild-born steelhead to conclude that each wild female adult brought into the hatchery would produce 4–10 times as many granddaughters (i.e., F_1 offspring of naturally spawning, hatchery-produced females) as wild females not brought into the hatchery had they been allowed to spawn naturally. In both of these studies, however, the response of the natural population in the absence of the hatchery program remains in question. The significant increase in redd abundance in the Hamma Hamma River in the face of stable or declining (nonsignificant) abundance in the three control streams makes this the first study to demonstrate an increase in natural spawning while accounting for spatial and temporal variability that can lead to changes in natural spawner abundance.

The approach of collecting embryos from wild steelhead redds appears to have represented a larger portion of the gene pool with a lesser demographic risk to the natural population than would have been possible with a more conventional approach. To explain, the project removed a total of 10 829 embryos (equivalent to the fecundity of roughly three females) from natural redds from 1998 through 2001. Kuligowski et al. (2005) showed that a subsample of the 4683 embryos collected in 1998 from eight redds descended from five different females and 16 different males. The embryos not removed may still have contributed to natural production. The more conventional approach of collecting adult broodstock and spawning them in the hatchery would have required the removal of approximately 15 females (45 000 to 60 000 eggs) and approximately 45 males to obtain a similar number of parental contributors, based on the number of redds sampled ($N = 25$) between 1998 and 2001. The smolts produced would either have to be released into the Hamma Hamma River, which would far exceed carrying capacity, or be removed from the population altogether. The embryo collection approach has been used in other conservation hatchery programs, but it is recognized that it may not be practical to collect the much larger number of eggs required for large-scale hatchery programs that rear and release tens of thousands of fish or more.

Fig. 6. Point estimates of the number of redds constructed by wild (solid bars), smolt release group (SRG, open bars), adult release group (ARG, stippled bars), and unknown origin (striped bars) steelhead in the Hamma Hamma River from 2002 through 2006. Estimates were made by multiplying the annual proportion of adults in each category observed during snorkel surveys by the total number of redds observed by foot surveys.



The adult reintroduction strategy produced a greater number of spawners, the majority of the redd production, and did so with fewer natural embryos removed from the wild than the smolt release strategy. The escape of some of the SRG from the John Creek facility and unknown smolt-to-adult survival rates make it difficult to calculate the number of embryos needed to produce a redd from the SRG strategy. A reasonable smolt-to-adult survival rate might be 2%–4% (cf. Ward 2000), compared with >90% smolt-to-adult survival rate in the hatchery for fish allocated to the ARG. The estimates of redd construction from the two groups clearly reflected the greater short-term demographic boost to the population from the adult release strategy. The far fewer number of embryos required to produce an equal number of spawning adults certainly lessens the demographic impact on the natural population.

The greater survey frequency in the Hamma Hamma River during the supplementation phase did not bias the analysis of redd abundance towards counting more redds in the Hamma Hamma River during the supplementation period. The strongest correlation between survey frequency and redd abundance was a nonsignificant negative one in the Hamma Hamma River during the presupplementation phase. All of the correlations for the other populations were slightly positive, but none were significant. Where evaluated, steelhead redds have been found to be visible for at least 1 week, and the great majority of redds are still visible after 2 weeks (Freymond and Foley 1985; Gallagher and Gallagher 2005; T. Johnson, unpublished data). Redd survey frequency in the Hamma Hamma River during the presupplementation period was approximately weekly and therefore sufficient to quantify redd abundance. Furthermore, the Dewatto and Duckabush rivers had greater survey frequencies during the supplementation period, so any potential bias associated with increased survey frequency would have tended to obscure rather than amplify the significant interaction between population and supplementation phase that we detected.

Although the adult release strategy provided the greater demographic boost, other trade-offs make it difficult to recommend one strategy over another. First, the reproductive success of hatchery-reared steelhead from natural-origin broodstock (similar to our SRG) can exhibit lifetime reproductive success that is similar to wild fish (Araki et al. 2006). Comparable reproductive success from the ARG is far less certain. For example, naturally spawning farmed Atlantic salmon (*Salmo salar*) have very poor reproductive success, perhaps caused by many generations of intense artificial selection (not a factor in our study) and full-term hatchery rearing experience (Fleming et al. 2001). Siblings of the steelhead observed in this study were closely examined for breeding behavior in a spawning channel and were found to be very successful at constructing nests and depositing eggs, and DNA pedigree analyses revealed that all females and 23 of 24 males contributed to fry production (Berejikian et al. 2005). However, the overall egg-to-fry survival rate was approximately 25% in the absence of any predators. It remains unclear how spawning density, spawning channel conditions, and gamete quality may have contributed to this result.

Second, the observed assortative pairing and its underlying causes raise interesting questions with respect to the potential contributions of the adult release strategy. The advanced spawn timing was an environmentally induced artifact of full-term rearing in the hatchery and exemplifies the phenotypic plasticity in this trait. One goal of a conservation hatchery program is to have hatchery-origin and wild fish interbreeding and for both groups to exhibit a natural level of fitness. If the current modal spawn timing of the wild population represents a naturally selected optimum trait distribution, then early-spawning females may have lower fitness owing to greater embryo mortality. Alternatively, to the extent that past harvest pressures have eliminated or reduced the early spawning portion of the population, early-spawning ARG females may function to recover historic diversity in spawn timing, and offspring of early-spawning females may fill a vacant niche and contribute to population productivity and life history diversity. Early-emerging fry could have an early growth and competitive advantages over later-emerging fry (Chandler and Bjornn 1988; Einum and Fleming 2000). However, embryonic developmental rate is positively correlated with temperature (Billard and Jensen 1996), which increases as the spawning season progresses. Therefore, the approximately 3-week difference in median spawn timing would actually result in less than a 3-week difference in median emergence timing and would tend to temper the effects of spawn timing differences. The absence of information on the reproductive success of the ARG fish in the natural environment and genetic concerns (e.g., domestication selection) associated with full-term captive rearing suggests that further use of this approach continue to proceed with caution.

As demonstrated in this and the aforementioned studies, conservation hatcheries might reasonably be expected to maintain or increase population abundance and maintain existing levels of genetic variability in the short term (which we will address in a future publication) to buy time until the factors causing population declines can be identified and addressed. A more ambitious and far less certain expectation for conservation hatcheries is to contribute to increasing the productivity of natural populations experiencing a positive relationship between population growth rate and density (e.g., depensatory mortality). Depensatory mechanisms may function to inhibit recovery of animal populations or increase the likelihood of extinction (Courchamp et al. 1999) and may include skewed sex ratios, nonlinear response of predation, nutrient limitation related to scarcity of spawner carcasses, and reproductive inefficiencies. Evidence for depensation has been detected for Pacific salmon (Myers et al. 1995). Thus far, no study, including this one, has empirically identified such a mechanism or the potential to increase natural population productivity through artificial propagation. To determine the impact of the hatchery program on natural population productivity, the release of hatchery fish will need to be terminated and the supplemented and control populations monitored for through the F_2 generation; this is the plan for the program evaluated in the present study.

To meet their goals, conservation hatcheries must strike a balance between increasing production and minimizing genetic, ecological, and demographic risks. Goodman (2004) noted that the idea of supplementation (as opposed to production hatcheries) did not arise from an inability to produce or dissatisfaction with the ability of hatchery programs to produce fish. It came out of conservation concerns for the wild stock. Moving towards a situation that is less risky for wild stocks almost invariably means reducing the potential of the hatchery stock to increase abundance in the short term. For example, release of smaller fish may reduce the potential for predation on wild fish, but smaller fish may not survive as well to adulthood. Releasing fewer hatchery fish will undoubtedly reduce the potential for competition that has been documented in natural streams (Nielsen 1994; McMichael et al. 1999), once again at the expense of adult production. These types of operational changes will reduce the impacts of hatchery fish on natural stocks; after all, the extreme example is the complete absence of hatchery fish. A major question has been whether hatcheries operated in a conservative fashion can substantially boost the number of naturally spawning adults (e.g., Oosterhout et al. 2005). The results of this study suggest they can.

Acknowledgements

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PERSPECTIVE / PERSPECTIVE

Models and indicators for assessing conservation and fisheries-related effects of marine protected areas

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Abstract: Two kinds of approaches have been used for assessing conservation and fisheries-related effects of marine protected areas (MPAs): (*i*) statistical modelling based on field data and (*ii*) mathematical modelling quantifying the consequences of MPAs on the dynamics of populations, communities, and fisheries. Statistical models provide a diagnostic on the impact of MPAs on the ecosystem and resources; they are also needed for devising and assessing sampling designs for monitoring programs. Dynamic models enable exploration of the consequences of MPA designs and other management policies. We briefly review how each of these approaches has been implemented up to now in the literature and identify potential indicators of MPA effects that can be obtained from each approach to provide scientific advice for managers. Methodological gaps that impede the assessment of MPA effects and the construction of appropriate indicators are then discussed, and recent developments in this respect are presented. We finally propose ways to reconcile the two approaches based on their complementarity to derive suitable indicators to support decision making. In this respect, we suggest in addition that MPA managers should be associated from the beginning to the design and construction of indicators.

Résumé : Deux sortes d'approches sont utilisées pour évaluer les effets des aires marines protégées (AMP) sur les pêcheries et la conservation biologique : (*i*) la modélisation statistique de données de terrain et (*ii*) la modélisation mathématique qui quantifie les conséquences des AMP sur la dynamique des populations, des peuplements et des pêcheries. Les modèles statistiques fournissent un diagnostic sur l'impact des AMP sur les écosystèmes et les ressources; ils sont également nécessaires pour mettre au point et évaluer des protocoles d'échantillonnage pour les programmes de suivi. Les modèles dynamiques permettent d'explorer les conséquences de différentes configurations de AMP et d'autres mesures de gestion. Nous faisons une brève revue bibliographique des applications de chacune de ces approches et identifions des indicateurs potentiels des effets des AMP, tels qu'ils peuvent être obtenus par chaque approche, dans le but de fournir un avis scientifique aux gestionnaires. Nous discutons ensuite des faiblesses méthodologiques qui nuisent à l'évaluation des effets des AMP et à la construction d'indicateurs appropriés et nous présentons des développements récents en la matière. Pour finir, nous proposons des pistes pour réconcilier les deux approches sur la base de leur complémentarité, afin d'en déduire des indicateurs adéquats pour aider à la prise de décisions. Dans cette optique, nous suggérons de plus que les gestionnaires de AMP soient associés dès le départ à la mise au point et à la construction des indicateurs.

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Introduction

Marine protected areas (MPAs) are now considered as major tools for biodiversity conservation and for fisheries management. Quantitative targets have been set in several international agendas as to the coverage of a global network of MPAs to be reached in the next 10–15 years to protect biodiversity (2002 World Summit for Sustainable Development (www.un.org/jsummit/html/sustainable_dev/sustainable_dev.html), Convention for Biological Diversity (www.cbd.int)). Other instruments have been mandated to assist in the designation of sites to be protected (OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic (www.ospar.org/); European "Habitats Directive" (ec.europa.eu/environment/nature/ legislation/habitatsdirective/index_en.htm); the future Marine Strategy Directive (ec.europa.eu/environment/water/marine/ docs_en.htm)). With respect to fisheries management, the new European Common Fisheries Policy recommends the use of MPAs in the form of partial or total restrictions to fishing, and requires that the efficiency of these measures be evaluated through a set of biological, economic, and social indicators (eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=COM:2002:0186:FIN:EN:PDF). Likewise, the Program of Work for Protected Areas of the Convention for Biological Diversity called on parties to develop and adopt appropriate methods, standards, criteria, and indicators for evaluating management effectiveness and governance by 2008 and to assess at least 30% of their protected areas by 2010. In spite of the general pressure for implementing MPA networks, there remain large uncertainties as to the designation of sites according to biodiversity status, threats, and constraints linked with human uses.

Because MPAs aim at "preserving specific areas together with their overlying water, substrate and associated flora, fauna historical and cultural heritage" (Kelleher and Kenchington 1992), they are considered as a central element of ecosystem-based management (Agardy 2000; Browman and Stergiou 2004). Consistent with this definition, MPAs are taken in the present article in the wider sense of an area where fishing and other human activities are restricted, even partially and (or) temporarily. Management goals for MPAs are various, including conservation and heritage preservation, education and research, sustainable exploitation and promotion, or control of tourism, but biodiversity conservation and fisheries management are the main motivations for MPA establishment (Boersma and Parrish 1999; Salm et al. 2000; Claudet and Pelletier 2004).

The interest of MPAs as a management tool for sustainable fisheries management is still open to debate; some argue that MPAs should not be considered as the "one size fits all" solution to all fisheries problems (Hilborn et al. 2004; Kaiser 2005), whereas others claim that global fishery declines could be reversed by implementing large-scale networks of marine reserves (Gell and Roberts 2003). For some authors, there is no overwhelming evidence on the effectiveness of MPAs for ecosystem conservation, let alone for fisheries management (Russ 2002; Hilborn et al. 2004). Assessing effects of MPAs on ecosystems and fisheries in a reliable and unquestionable way is therefore important.

Methodologies for assessing the effectiveness of MPA management are in development, and several initiatives are being undertaken to evaluate them (Wells and Dahl-Tacconi 2006). In the present article, our interest is twofold. First, we review the methods that can be used to assess progress toward the achievement of ecosystem conservation and fisheries management objectives. Second, we discuss the ability of these methods to produce indicators for this purpose.

We particularly concentrate on fish populations and communities. By fish, we mean all macroinvertebrates and fish species, whether exploited or not. Economic and social effects, i.e., consequences of MPA on fishing and other human activities, will not be dealt with in this paper, although we are fully aware of their importance (see e.g., Pelletier et al. 2005; see also Perspectives section below).

Assessment is here understood as the main support to reliable, quantitative, scientific advice for management and decision making. A key component of this scientific advice is the provision of indicators. By indicator, we mean a function of observations or of the outputs of a model, which value indicates the present state and (or) dynamics of the system of interest (Food and Agriculture Organisation 1999). We are here interested at indicators aimed at testing hypotheses about conservation or fisheries-related effects of MPAs. The performance of such indicators lies mainly in their statistical properties and their sensitivity to the question addressed. To stress the importance of validating indicators through performance criteria, we distinguish metrics (biological responses observed or calculated at a given scale) and indicators (metrics displaying desirable performances for a given purpose, in this case for testing MPA effects). Although there are a number of references about indicators of fishing effects (Trenkel and Rochet 2003; Daan et al. 2005; Jennings 2005), there are surprisingly few articles quoting indicators of MPA effects (Ohman et al. 1998; Harmelin 1999; Amand et al. 2004). Aside from the peer-reviewed scientific literature, the MPA Management Effectiveness Initiative, formed in 2000 by The World Conservation Union (IUCN) World Commission on Protected Areas and by World Wildlife Fund, proposed sets of indicators to assess management effectiveness. The main objective of the MPA Management Effectiveness Initiative was "to develop a set of marine-specific natural and social indicators to evaluate MPA management effectiveness", based on both scientific and practitioner expertise. Results are presented in a guidebook aimed at helping managers and practitioners to better achieve the goals and objectives for which their MPA was created (Pomeroy et al. 2004). The guidebook provides clear insight into the construction of indicators, but it is not intended to propose assessment methods nor means to evaluate indicator performance. Thus, to our knowledge, there is currently no review and comparison of MPA assessment methods and of their ability to provide indicators of MPA effects for informing the decision-making process.

In the scientific literature, assessment of conservation and fisheries-related impacts of MPAs is generally achieved via two approaches: (*i*) empirical approaches based on statistical modelling of field data, used to test effects and provide diagnostics; and (*ii*) dynamic models of populations, communities, or ecosystems, generally used for policy screening and for generating hypotheses to be further tested in the field. These two approaches respectively relate to the two scales, local and system-wide, at which conservation and fisheries-related effects of MPAs operate. After MPA establishment, the ecosystem is first affected within the MPA at a local scale. In the case of multiple use MPAs (MUMPAs), fisheries-related effects may also occur in the partially protected area. If dispersion and migration patterns bring species outside of the MPA even temporarily, effects within the MPA will in turn affect both ecosystem and fisheries at a larger scale. MPA effects should thus be assessed at each scale (Guidetti 2007). These spatial scales are associated to specific time scales, depending on ecosystem connectivity and response to exploitation.

Empirical assessment methodology is briefly discussed by Russ (2002) and Willis et al. (2003*b*), among others. Pelletier and Mahévas (2005) reviewed dynamic models used for MPA analysis and discussed model assumptions and their consequences on model outputs. But we could find no reference addressing and discussing both empirical assessments and dynamic modelling of MPAs.

In this article, we first provide a brief description of state-of-the-art approaches for the assessment of MPA effects on fish assemblages and fisheries. Assessment methods are then discussed in the light of their ability to lead to indicators of MPA effects. In a third step, we identify methodological gaps in current approaches and propose possible ways for improving MPA assessment, in particular regarding the development of indicators tracking progress toward the achievement of management objectives. We finally investigate how the two approaches may benefit each other, with the ultimate aim of providing scientific advice to support decision making by MPA and fisheries managers.

Current approaches to assessing MPA effects

As mentioned above, two kinds of approaches have been envisaged to assess conservation and fisheries-related effects of MPA: (*i*) dynamic models depicting temporal changes in the spatial dynamics and structure of the populations, communities, or ecosystems; and (*ii*) empirical approaches based on statistical modelling of field data. The latter should lead to defining empirical indicators and sampling designs for long-term monitoring programs, whereas the former enables exploration of issues related to MPA design and its consequences on the dynamics of populations and fisheries. These can also provide reference points against which system dynamics can be gauged.

Assessing MPA effects from dynamic models

A number of dynamic models of fisheries and exploited populations have been developed in the last decade to evaluate conservation and fisheries-related effects of MPAs (Gerber et al. 2003). In the present article, we propose a classification of existing models based on the extensive review of Pelletier and Mahévas (2005), mainly to serve as a basis for the discussion on indicators (see section below on Which indicators for MPA assessment?). Models were classified into five types, ranging from simple to complex models. First, nonspatial, single-species models often rely on logistic population growth and assume instantaneous dispersion of fish over the entire fishery area and uniform fishing mortality. They are used to investigate permanent no-take reserves covering a fraction of the ocean (e.g., Lauck et al. 1998; Mangel 1998; Hastings and Botsford 1999). Second, source–sink models make assumptions about larval dispersion schemes, considering local dynamics in each patch; they enable exploring no-take reserve designs in terms of number, size, and location in source versus sink patches (e.g., Crowder et al. 2000; Tuck and Possingham 2000; Sanchirico and Wilen 2001). From the literature, these two kinds of models are used as conceptual tools to yield general ideas about MPA effects. A discussion about the shortcomings and advantages of simple models in theoretical ecology may be found in May (2004). In practice, these aggregated models cannot address some issues raised by policy makers regarding the management of real fisheries, such as MPA location and design of MUMPAs. Similarly, single-species models ignoring the demographic structure of the population provide little insight about the effectiveness of MPAs aimed at protecting juveniles or spawners. Third, spatially explicit demographic models depict growth, reproduction, fishing, and natural mortalities, as well as fish movement (e.g., Polacheck 1990; Walters et al. 1993; Pelletier and Magal 1996). MPA designs investigated include number, size, location of MPAs, and possibly temporary closures in the case of models with intra-annual dynamics. Fourth, spatially explicit fisheries models include additional detail concerning exploitation, in particular, effort may be described in terms of gears, vessel number and characteristics, and fleet dynamics (Walters and Bonfil 1999; Holland 2000; Pelletier and Mahévas 2005). These models are appropriate for investigating MPA designs other than permanent no-take zones and for appraising the impact of MPAs upon population structure; they also account for restoration through enhanced reproduction and recruitment. MPA designs aimed at protecting sensitive stages of populations, possibly on a seasonal basis, may be investigated, although there are few published examples (see papers cited above, and Drouineau et al. 2006). Additionally, spatially explicit fisheries models permit the investigation of more elaborate policies, including MPAs targeting particular fishing activities or gears, combined with other regulatory measures such as effort controls. They are also needed for exploring mixed (multispecies, multifleet) fisheries issues, such as technical interactions and discards. Finally, they may account for fishers' response to policy implementation, which is particularly relevant in the case of MPAs. In general, these models do not address the consequences of MPAs at the community level. In contrast, trophodynamic models describe the state or dynamics of communities or ecosystems based on trophic interactions. Interactions are modelled at the scale of either age- and size-specific fish schools (Shin and Cury 2001) or functional groups using biomass flows and mass–balance equations, such as in ECOPATH (Christensen and Pauly 1992) and in ECOSPACE, a spatially explicit and dynamic model that also accounts for dispersal and migration (Walters et al. 1999). Such models have been used a few times for exploring the effectiveness of permanent no-take zones (Walters 2000; Watson et al. 2000; Shin and Cury 2001). The complexity of trophic interactions makes it difficult to explicate additional model components such as demographic processes and exploitation; therefore, they cannot be easily used for exploring MPA designs and for comparisons with other management measures (but see Beattie et al. 2002 for trawl-exclusion scenarios). Predator–prey models have also been developed lately (Boncoeur et al. 2002; Micheli et al. 2004*a*; Mangel and Levin 2005).

Simple conceptual models in the first two categories (e.g., Hastings and Botsford 1999, 2003) are aimed at understanding possible consequences of MPAs and providing theoretical insight on the dynamics of resources and exploitation under MPA management. They are less demanding in term of input data and model implementation and less prone to problems of structural stability and parameter identifiability. More complex models such as spatially explicit models, mixed fisheries models, or trophodynamic models allow the consideration of additional key processes and are used for policy screening that can form the basis for decision support systems. However, because they have more parameters and are data-driven, they are more prone to uncertainties and their outputs should be carefully analysed in this respect (see Pelletier and Mahévas 2005 for a discussion). For the purpose of defining indicators for MPA effects, simple conceptual models are helpful for appraising in a simple way consequences of MPAs on fisheries and marine populations, while data-driven models will provide quantitative indicators on the dynamics of resources and exploitation in real cases. To be able to provide indicators that can be subsequently used by managers for adaptive management, models should capture the various components of fishing mortality, as well as the zoning of resources and fishing, so that scenarios including changes in fishing regulations, e.g., concerning gears, zones, or vessels, can be evaluated.

Metrics common to all models are total catch, total abundance, and total biomass. The other metrics differ depending on model state variables, assumptions, dimensions, and parameterization, e.g., is the model spatially explicit, does it consider age or size structure, are interspecific relationships accounted for or not, etc. For instance, total catch calculated from a demographic population model is not the same metric as total catch obtained from a trophodynamic model. Although not surprising, this stresses the fact that the way a metric is estimated or calculated influences its properties. Moderate differences in model assumptions may lead to different and sometimes contradictory results (not detailed here, see Pelletier and Mahévas 2005 for examples). Hence, defining a metric must include the specification of the model from which it is calculated: assumptions, processes considered, and parameter values. Evaluating the precision, accuracy, and sensitivity to MPA effects of each metric would require the implementation of each model and carrying out sensitivity analyses and stochastic simulations. Ideally, the publication of a model should include such evaluations, and comparative analyses between models and metrics may then be achieved. But this is tedious and thus rarely done in practice (see section below on Possible contributions of dynamic models to empirical analyses).

Finally, it should be noted that most published models are neither fitted nor calibrated from real data (see section below on Improving methodology for MPA assessment), thereby providing little information about the relevance and robustness of the metrics in real situations.

Assessing MPA effects from the analysis of field data

Many studies have assessed the impact of MPAs on fish populations and on marine organisms (see e.g., reviews in Russ 2002; Halpern 2003; Micheli et al. 2004*b*). The majority of these studies pertains to no-take reserves aimed at biological conservation in coral reef ecosystems (see García-Charton et al. 2000; Sanchez-Lizaso et al. 2000; and Planes et al. 2006 for reviews focused on Mediterranean ecosystems). In this section, the term reserve is preferred to MPA because published studies concern no-take reserves (unless otherwise specified). Most papers are interested in assessing direct effects of reserves, i.e., restoration of populations and assemblage structure within the reserve, which is commonly achieved by analysing biological responses (such as densities, biomasses, mean sizes, species richness, and other diversity indices) to evidence differences between the reserve and a comparable zone. Early references relied on descriptive analyses (e.g., Alcala 1988), while most others use statistical modelling of biological responses. The techniques most often used are parametric and nonparametric univariate tests (Rakitin and Kramer 1996) and univariate general linear models involving design factors such as location and time (e.g., Babcock et al. 1999; Chiappone et al. 2000; Willis et al. 2003*a*). In such univariate models, tests are carried out separately for each metric, e.g., the density of Serranids or the overall mean size of fish. Changes in assemblage structure are examined more rarely; early papers mostly relied on descriptive multivariate methods that do not allow statistical inference (Dufour et al. 1995; Russ and Alcala 1998; Paddack and Estes 2000), although a few recent papers use multivariate inferential methods (Micheli et al. 2005; Ceccherelli et al. 2006; Claudet et al. 2006).

The examination of the literature reveals that significant differences are obtained for some particular species (e.g., Bell 1983; Paddack and Estes 2000; García-Charton et al. 2004), taxonomic families (e.g., Jennings et al. 1996; Letourneur 1996; Wantiez et al. 1997), or other groups of species, e.g., large predators (Russ and Alcala 1996; Chiappone et al. 2000). Significant differences are more likely observed when the reserve has already been in place for several years (Alcala 1988; Paddack and Estes 2000) and when fishing pressure is high before MPA establishment and outside the MPA (Côté et al. 2001; Micheli et al. 2004*b*). However, in a number of cases, nonsignificant results were obtained for a substantial number of species, genera, or taxonomic families (e.g., Rakitin and Kramer 1996; Chapman and Kramer 1999; Paddack and Estes 2000), in particular in recently established reserves (Alcala 1988). This lack of significance was also pointed out by Russ (2002) and Willis et al. (2003*b*).

Halpern (2003) compiled the results from a large number of empirical studies and found that reserves were associated with higher values of biomass, density, mean size, and species diversity, in terms of overall trends and for four functional groups including herbivores, planktivores–invertebrate eaters, carnivores, and invertebrates. Micheli et al. (2004*b*) conducted a meta-analysis of published studies of changes in the abundance of fish assemblages within no-take reserves. They evidenced differences in species response according to trophic level, exploitation rate, and duration of protection and showed that a substantial fraction of species was negatively affected by protection, illustrating indirect effects of MPAs. Similar results were obtained by Guidetti and Sala (2007) for Mediterranean fish assemblages. Claudet et al.

(2008), based on meta-analysis of original data sets from European Mediterranean and eastern Atlantic MPAs, upheld that the response of commercial species to protection depends on reserve size and that older marine reserves are more efficient than newly established reserves at increasing commercial fish size and maintaining fish species richness.

In another review about the empirical assessment of MPAs, Pelletier et al. (2005) identified the metrics used for assessing conservation and fisheries-related effects of MPAs and scored their performance as indicators according to the relevance and effectiveness criteria proposed by Nicholson and Fryer (2002). They showed that several effects were still rarely addressed, mostly long-term effects, but also effects linked to trophic interactions, density-dependent changes, and protection of endangered species. Effects at the community level were less studied than effects at the population level, and habitat-related effects were not often investigated. Many metrics have been contemplated for studying MPA effects, but overall, few of them appear to be relevant and effective. These findings differ to some extent from Halpern's (2003) results, mainly because the analysis is restricted to inferential assessments, thereby granting more weight to statistical significance. In Halpern's study, descriptive analyses were handled in the same way as inferential ones, since meta-analyses allow for use of noninferential results (whereas the statistical significance of the meta-analysis is reported). The results of Pelletier et al. (2005) corroborate and systematize other recent reviews of empirical studies that point out a low level of empirical evidence (based on statistical significance) for MPA effects (Russ 2002; Willis et al. 2003*b*), probably reflecting in some instances the lack of appropriate controls and poor experimental designs. Note that sometimes there may also be no MPA effects due to MPA recentness, lack of enforcement, or poor MPA design. Otherwise, the lack of statistical significance may be explained by several weaknesses encountered in a number of studies. The first weakness pertains to the lack of initial evaluation, as in many studies, the initial state of the fish community was not assessed before MPA establishment. Abundance and other biological variables inside the MPA were compared with those in one or several control zones, i.e., from a control–impact design (e.g., Harmelin et al. 1995; Letourneur 1996). Spatial and temporal heterogeneities of ecosystems lead to confusion of protection effects with environmental effects, such as the relationships between species and habitat structure (Samoilys 1988; Garcia-Charton and Perez-Ruzafa 1999, see also below). This makes it necessary to rely on designs including measurements before and after establishment of the MPA and inside and outside of the MPA, i.e., before–after control–impact (BACI) designs (Osenberg et al. 1994; Underwood 1994). Although such designs become more frequent, there are much fewer published examples than for after control–impact (ACI) designs.

A second issue relates to habitat effects. Habitat is determined by explaining the spatial distribution and structure of fish communities (McCoy and Bell 1991; Sale 1998) and should thus be accounted for when comparing biological responses in distinct zones. Relatively few assessments have explicitly considered habitat. In several instances, differences in densities were tested by habitat type (e.g., Letourneur et al. 1997). Paddack and Estes (2000) compared fish assemblages between sites while accounting for substrate composition. Sometimes, an additional factor related to habitat was included in the model, like depth (Bell 1983; Garcia-Rubies and Zabala 1990; Kelly et al. 2000), reef type (Chapman and Kramer 1999), geographical orientation (Micheli et al. 2005), or some other definition of habitat (McCormick and Choat 1987; Castilla and Bustamante 1989; Ferraris et al. 2005). Recent works by Garcia-Charton et al. (2004), Micheli et al. (2005), and Claudet (2006) show how habitat effects and protection effects may interact and complicate the evaluation of conservation effects of MPA. These studies indicate the importance of explicitly considering habitat effects to avoid spatial confounding and to increase the strength of statistical inference when assessing MPA effects.

The third issue relates to the diagnostic of MPA effects. Direct effects generally assessed by comparing densities, biomasses, mean size, or diversity indices between the reserve and the unprotected area. Statistical tests are carried out independently for some species or species groups of interest. These results are helpful for better understanding the response of some particular species to reserve protection, but they do not provide a synoptic view of the impact of the reserve. Besides, they do not allow comparing the sensitivities of different fish community components to protection, thereby impeding the construction of ecosystemic indicators for MPA assessment. Evaluating effects at the fish community level would be more desirable to provide scientific elements for an ecosystem approach to management (Botsford et al. 1997; Jennings and Kaiser 1998) in the context of MPAs.

Which indicators for MPA assessment?

Candidate indicators

In the light of the previous section, we compiled a number of metrics that can be considered as candidate indicators for the MPA effects of interest: protecting critical spawning stock biomass, rehabilitating population demographic structure, restoration of or changes in assemblage structure, exportation of biomass, protecting biodiversity, indirect effects on algae and invertebrates, enhancing fisheries yield, increasing population stability and resilience (Table 1). Model-based indicators are based on outcomes from dynamic models, while empirical indicators rely on the analysis of field data.

The properties of model-based indicators depend on model assumptions and on the algorithms used (see previous section). Accordingly, data requirements depend on the model. Most dynamic models involve describing population dynamics and exploitation. Population dynamics require biological parameters and, in the case of spatially explicit models, information on the spatial distribution and movements of organisms. Exploitation is parameterized through effort and catch data regarding the resources at stake. These data may be available in many documented fisheries, although information on spatial dynamics is often lacking. However, they will be nonexistent in many countries or for highly multispecific fisheries. This is particularly problematic because many MPA issues arise in coastal areas where exploited species are numerous. The cost of gathering the information needed for parameterizing and calibrating these models is

Table 1. Synthesis of candidate indicators for conservation and fisheries-related effects expected from marine protected area (MPA) establishment.

Effect	Empirical indicator	Model-based indicator
Short-term		
Protecting critical spawning stock biomass	Total biomass; biomass per family; total density; density of fishable species; density per trophic group, family, or species stage; size distribution of species; **biomass per species or genus; density per species or genus; CPUE per species**	Biomass (total or per patch); abundance (total, per patch or per subpopulation); spawner abundance and biomass; risk of population collapse; asymptotic growth rate[a]
Rehabilitating population demographic structure	Size distribution of species; **mean size per species or genus; biomass per species or genus**	Spawner abundance and biomass; stable age distribution[a]
Restoration of or changes in assemblage structure	Density profile per species; **species richness per family**	Size or biomass spectra; catch or biomass per community component[b]
Medium-term		
Exportation of biomass	Movement patterns; home range; site fidelity	Abundance (per subpopulation or per patch); catch per patch; biomass (per subpopulation or per patch)
Protecting biodiversity	Total species richness; **other diversity indices**	Catch or biomass (total or per component); size or biomass spectra
Indirect effects on algae and invertebrates	Benthic cover; **density per species or genus**	**Abundance of invertebrates; abundance of algae**
Enhancing fisheries yield	**CPUE per species**	Catch (total or per fleet); catch variation; effort-related metrics; economic metrics; short-term yield; equilibrium yield[c]
Increasing population stability and resilience	**Density variation; CPUE variation**	Risk of population collapse; asymptotic growth rate[a]

Note: Additional metrics were suggested (bold type) when no metric could be identified from the literature or when they were obviously underrated from existing literature. Unless specified, model-based metrics may be obtained from several models. Short-term refers to the year scale (1–3 years); medium-term refers to generation time.

[a] For Leslie models, see Pelletier and Magal (1996) for an example.

[b] Trophodynamic models.

[c] Yield-per-recruit model.

generally high, since information has to be collected at the scale of the fishery for both resource and exploitation. To achieve a given precision in model-based indicators, this cost is determined by the sensitivity of model-based indicators to uncertainties in inputs and to changes in exploitation following MPA implementation, which totally depends on (*i*) model structure and model complexity and (*ii*) the precision and accuracy of model parameter estimates. The sensitivity of single-species fisheries models to such uncertainties and their implications for assessing alternative management options have long been studied (Pelletier and Gros 1991; Pelletier and Laurec 1992; Kell et al. 2006), but in the case of MPAs, studies are scarce (Drouineau et al. 2006). We are aware of no such studies for multispecies models.

With regard to empirical indicators, their properties depend on both experimental design and observation techniques. For example, overall fish abundance estimated from underwater visual censuses (UVC) following a given observation design is not the same metric as overall fish abundance obtained from experimental fishing or from UVC but from another design. The cost of gathering the information needed for calculating empirical indicators depends on the precision required for the indicator, which in turn depends on the size of the effect to be detected, on sample size, and on the sensitivity of the indicator to this effect, i.e., the relevance of the indicator according to Nicholson and Fryer (2002). There is thus no general rule as to the cost of data collection for empirical indicators, although general qualitative guidelines are given in Pomeroy et al. (2004). Hence, if a given set of information may be used to estimate several indicators, it will thereby result in decreased costs per indicator. For instance, fish density, biomass, and mean size may be estimated from the same set of UVC data. This possibility should be taken into account when selecting empirical indicators. Another option is to prefer indicators based on data less demanding in terms of observation skills or human resources. For instance, Graham et al. (2005) proposed size spectra at the scale of the fish assemblage as an indicator of the effects of fishing on coral reef fish assemblages, because size estimation is an easily trainable technique.

Capturing the various effects of MPAs requires several indicators. Regarding fisheries management, metrics based on spatially explicit, stage-structured fisheries models are necessary to appraise the consequences of MPA designs and adjunct fisheries management measures at the population level. Abundance, biomass, and age distribution indicate population state, while asymptotic growth rate, risk of collapse, and abundance variations reflect its dynamics (see Pelletier and Mahévas 2005 for other metrics of population and catch dynamics). While most dynamic models focus on abundance and catch or yield, yield enhancement is not often studied from field data, and there is still little empirical evidence for overall yield increase following MPA establishment (McClanahan and Mangi 2000; Russ et al. 2004; Goñi et al.

2006). As underlined by Russ (2002), "There is a plethora of reviews on what marine reserves could do as fisheries management tools. Yet there is a distinct paucity of empirical studies demonstrating what they can do." As for conservation issues, these are mostly tackled through experimental field data. Total biomass, density of fished species, predator density, size distribution per species, and to a lesser extent total species richness were the most effective families of metrics in Pelletier et al. (2005) (Table 1). Several empirical metrics may be relevant for a given effect, and their performance needs to be further assessed. In addition to species richness, which depends on the extent of the area surveyed, we suggest that other diversity indices should be more often used. In the case where fishing is not totally prohibited within the MPA (e.g., MUMPAs), catch per unit effort (CPUE) provides interesting metrics if the calculation yields accurate abundance indices, which requires good appraisal of the location and magnitude of fishing effort. As for dynamic models, models accounting for species interactions are necessary to evaluate effects at the community level, e.g., trophic cascade effects (Pinnegar et al. 2000). Metrics resulting from these models include catch and biomass levels and profiles over trophic groups.

Scale dependency

Although apparently similar in essence, i.e., mostly based on abundance indices, model-based and empirical indicators differ because they pertain to distinct spatial, temporal, and ecological scales (see Hastings 2004 for a discussion on the disconnection between time scales in empirical and theoretical studies). On the one hand, empirical approaches are strongly constrained by observation scale. Most studies rely on UVC or experimental fishing, are conducted locally, and provide snapshot observations. But these data enable the observation of every species and the estimation of metrics at the community level. On the other hand, dynamic models focus on system-wide effects, whether the system refers to the fishery, the fish community, or a single fish population. They encompass a longer time horizon and may integrate ecological scales from the individual up to the community. They thus provide insight into the sustainability of resources and the exploitation and possible yield enhancement through MPAs, which are not local issues.

MPA effects could be studied from large-scale surveys or joint analyses of large-scale data (e.g., Jennings et al. 2002; Link et al. 2002; Methratta and Link 2006). Increasing the temporal range of the study would require accounting for dynamics in empirical assessments and adapting sampling designs.

Reference points

Sainsbury and Sumaila (2003) and others define reference points as desired targets and limits for an indicator. The availability of reference points with threshold and limit values is considered a desirable property for indicators (Nicholson and Fryer 2002; Rochet and Trenkel 2003).

In the case of dynamic modelling approaches, reference points may be provided through the model. The direction and magnitude of changes in indicators as a function of exploitation controls, e.g., MPA design, may be studied. As such, models provide indicators that are appropriate to assess fisheries-related effects at the scale of the whole fishery system. However, indicators and reference points are entirely dependent on the model.

In the case of empirical assessments, there is no such provision of reference points. In our view, this is not problematic because the role of a reference point is to provide values against which indicators can be gauged to provide a diagnostic. In this respect, reference points are provided by values of indicators in control areas, i.e., before MPA establishment and outside the MPA. Although empirical indicators do not allow one to anticipate future changes in the ecosystem and fishery, they may still be appropriate to address local issues in fisheries management, e.g., artisanal fishers operating in the vicinity of the MPA or in a MUMPA.

Finally, MPAs can (and should) themselves become, in the long term, control areas for the evaluation of population and ecosystem effects of fishing (the role of MPA as a natural laboratory). They then allow for experimental approaches (including actively adaptive management) at the ecosystem scale (Walters 1997; Castilla 2000). However, the ecosystem restored in the MPA may not resemble the pristine ecosystem because of the irreversibility of changes. Historical data (Jackson et al. 2001; Sáenz-Arroyo et al. 2005; Lozano-Montes et al. 2008) coupled to monitoring before and after MPA establishment may then help to understand the causes of ecological changes at several scales, both retrospectively and within the MPA.

Improving methodology for MPA assessment

The examination of the current status of MPA assessment and previous discussion about possible indicators of MPA effects reveal that methodologies for assessing conservation and fisheries-related effects of MPA could be improved. This would facilitate estimating appropriate indicators. Concerning empirical assessments of MPA effects, experimental design is a major area of improvement. There are still few examples of properly replicated sampling designs in MPA assessment (Fraschetti et al. 2002). Because many different processes operate simultaneously to generate spatial and temporal variability in populations, assessing these effects requires multifactorial sampling designs. Beyond-BACI designs provide such a framework (Underwood 1992, 1994; Osenberg et al. 1994). Inference is possible with these designs if data are sampled at several times before and after MPA establishment, both within the MPA and in several control locations outside. Multiple controls are necessary to avoid confounding natural spatial variability with MPA effects or missing other consequences of management. The significance of the difference between MPA mean and the mean over control locations is then assessed with reference to the natural variability of the system, estimated by the differences among controls. In contrast, using a single control location may lead to erroneous assessments. Edgar et al. (2004) and Kendall et al. (2004) provide recent examples of baseline assessment before MPA establishment or enlargement. There are also several examples of assessment of MPA effects based on ACI designs with multiple control sites (Garcia-Charton et al. 2004; Micheli et al. 2005; Ceccherelli et al. 2006).

There are other issues pertaining to sampling design and monitoring. For instance, MPAs are increasingly envisaged under the form of reserve networks, which implies both local and regional scaling for sampling designs. Sampling designs and performance of indicators in terms of precision and statistical power may be investigated and optimized using simulations and comparative approaches across case studies (Benedetti-Cecchi 2001; Sala et al. 2002). The choice of an observation technique also bears consequences on the precision and accuracy of indicators and on monitoring costs and sampling designs (Willis et al. 2000, 2006). Underwater video is a promising means for observing fish communities, macrofauna, and benthos, but is still rarely used for MPA studies (Rouphaël and Inglis 2001; Willis et al. 2003*a*; Denny and Babcock 2004). It provides a complementary picture of benthos and communities with respect to UVC and experimental fishing (Willis et al. 2000; Langlois et al. 2005, 2006; Stobart et al. 2007). Compared with UVC, it implies different costs and resources for observation, which may in certain circumstances be more adequate for monitoring (example at www.aims.gov.au/pages/research/reef-monitoring/methods.html; D. Pelletier, unpublished data).

A second area of improvement relates to habitat considerations. Habitat is a crucial source of spatial variability for fish communities (Sale 1998). Ignoring habitat when assessing MPA effects results in increased residual variability and less statistical power. Sampling designs should account for such confounding factors; ideally, habitat should be monitored at the same time as fish communities (García-Charton et al. 2000; Stewart-Oaten and Bence 2001). Information on habitat and more generally on the different components of spatial variability should be introduced in models, thereby reducing variability (García-Charton et al. 2004). In Ferraris et al. (2005), multivariate habitat data collected at the same time as fish counts were incorporated in the model for assessing the impact of fishing in a reserve. This approach is suited for considering habitats at a small scale and for taking into account several variables in the definition of habitat. In this case, habitat data can be used for defining habitat types based on multivariate and cluster analyses. Alternatively, the survey of fish and macrofauna can be designed a priori to cross protection factors and habitat factors. This is appropriate, for instance, when the habitat proxy is monofactorial and at an intermediate scale that is compatible with design and replication requirements (e.g., Micheli et al. 2005).

A third area of improvement lies in more holistic approaches to evaluate MPA effects. Effects are mostly evaluated from univariate approaches, i.e., for a single species or species group, and for a single variable, e.g., density or biomass, at the time. Consequently, an overall diagnostic about MPA effects cannot be established, nor can the performances of metrics be formally compared. Several approaches were recently proposed to address these problems. Hence, Ferraris et al. (2005) jointly modelled the densities of species groups pertaining to a range of demographic and trophic criteria to test the effect on the whole fish assemblage of fishing in a former reserve. This model was further developed by Amand et al. (2004) by considering in a single multivariate model several biological responses (density, species richness, mean size, and biomass) as a function of factors linked to reserve status and habitat. Results were used for comparing the sensitivities of the metrics to changes in reserve status. Begg et al. (2005) used a multivariate approach to find the demographic parameters that were sensitive to MPA status in the case of two coral reef fish species. Robust multivariate analyses, such as permutational analysis of variance (Anderson 2001) and multivariate regression trees (De'ath 2002), have been recently applied to the estimation of MPA-related effects (Langlois et al. 2005; Claudet et al. 2006; Ceccherelli et al. 2006).

Concerning dynamic modelling approaches, the usefulness of mathematical models for evaluating MPA effects is sometimes challenged: "theoretical models are useful in developing our ideas, but they are just that: ideas" (Willis et al. 2003*b*). From the existing literature, we generally agree that many models are theoretical contributions and that simple models published in well-known journals may have resulted in simplistic prescriptions, e.g., about the minimum size of no-take zones needed to protect fisheries resources, which in turn may hamper progress in marine conservation (Agardy et al. 2003). However, models are remarkable tools to evaluate MPA consequences at the scale of fisheries and ecosystems. In our opinion, the main area of improvement for these approaches lies in the development of models that achieve a trade-off between parsimony and complexity and are parameterized and calibrated against real data. More specifically, models are needed that explicate the spatial dynamics of population and exploitation at the scale of MPA design, including the seasonal scale when relevant, e.g., for temporary restrictions on fishing. Models should account for mixed fisheries and for fishers' response to MPA. They should allow for thorough investigations of MPA designs, including permanent versus temporary MPAs, partial restrictions of fishing activities, and reserve networks. They should also provide for other management measures, as MPAs are not the only management tool used in a given fishery. Several of these points were already raised by Sumaila et al. (2000). Pelletier et al. (2001) and Mahévas and Pelletier (2004) proposed a model (www.ifremer.fr/isis-fish) that incorporates most of these features. The model was compared with existing models in Pelletier and Mahévas (2005) and applied to coastal fisheries (Pelletier et al. 2007) and to the Bay of Biscay mixed fishery by Drouineau et al. (2006), who found that several MPA designs and improvement in trawl selectivity resulted in increased abundances for the modelled resources.

To be able to calibrate models against real data, we need appropriate information at the scale of the ecosystem and fisheries. Knowledge of spatial dynamics of population demographic stages, including early stages, is necessary, and some of these aspects are unfortunately still poorly known, but the need for a better appraisal of the spatial dynamics of exploitation should also be emphasized. Conventional fisheries statistics provide information with good spatial and seasonal coverage, but their interpretation may be difficult and spatial resolution may be limited (Verdoit et al. 2003). Additional information can be obtained through vessel monitoring systems (Murawski et al. 2005) and fishers interviews. Recent research projects (ec.europa.eu/research/agriculture/projects/qlrt_2001_01291_en.htm, www.mpa-eu.net/, www.um.es/empafish) have focused on these questions. In any

Table 2. Complementary aspects of empirical studies and dynamic modelling approaches with regard to the assessment of marine protected area (MPA) effects and subsequent provision of indicators.

Empirical study	Modelling approach
Local assessment	System-wide integration (fisheries scale – ecosystem scale – coastal management scale)
Snapshot information	Integrate knowledge about system components; transfer of local knowledge at the scale of the system
Formal testing of effects	Quantitative assessment of system dynamics
Field validation	Exploration of scenarios, e.g., MPA design, and hypotheses
Actual estimates of variance components and effect sizes	Possible projections in the future; generate hypotheses to be tested from field experiments
Control sites	Provision of theoretical reference points
Direct link with monitoring	Overall diagnostic on system

case, the model should be used to account for uncertainties, whether through simulation designs (e.g., Drouineau et al. 2006) or other techniques, e.g., risk analysis.

These modelling issues underpin the construction of model-based indicators, as reliable model outputs require models that are grounded with respect to real data.

Perspectives

The complementarity of empirical and model-based indicators

There is currently a gap between empirical studies and dynamic modelling approaches concerning MPA assessment. The latter may be deemed too theoretical by field ecologists (see previous subsection), whereas field data collected for MPA assessments are generally not used by modellers to calibrate models. Yet, in our view, dynamic models are indispensable to evaluate MPA consequences at the scale of fisheries and ecosystems and to provide corresponding indicators. The development of more realistic models should reduce this gap. We believe that empirical and model-based approaches to MPA assessment are complementary for several reasons (Table 2).

First, empirical approaches provide indicators that have traditionally focused on biodiversity conservation, the interest for fisheries management being more recent. Biodiversity may be directly observed at local scales from a variety of metrics, whereas indicators for resources and fisheries need to account for the dynamics at the fisheries level and for the spatial distribution of fishing effort, which is not a trivial issue for constructing empirical indicators. Therefore, conventional fisheries abundance indices are more often based on fisheries-independent surveys at the scale of the fishery, e.g., bottom trawl surveys used in assessment working groups in the International Council for the Exploration of the Sea (ICES, www.ices.dk/iceswork/ACOM.asp?topic=workinggroups, e.g., Anonymous 2006). Indices have also been calculated from models integrating population dynamics and fishing effort, e.g., models used for stock assessment in many international fishing agencies (ICES, Inter-American Tropical Tuna Commission). Recently fishery data collected at fine spatial scales have been used to analyse the effects of MPAs on fishing effort and catch (Murawski et al. 2005; Stelzenmüller et al. 2007).

Second, empirical approaches mostly provide indicators of the status of fish communities and resources. When inferential, these approaches lead to diagnostics based on statistical testing of hypotheses about indicators. In contrast, approaches relying on dynamic models enable the building of indicators of the dynamics of resources and fish communities. They generally do not provide for an inferential diagnostic but allow comparing the current assessment to alternative situations corresponding to other fishing pressures and other population dynamics. In some instances, the dynamics inherent in the model may lead to the definition of reference points (Mace 1994). Note that in empirical approaches, reference points may also be defined and estimated but in general require a long time series of data to appraise a variety of states of nature over time.

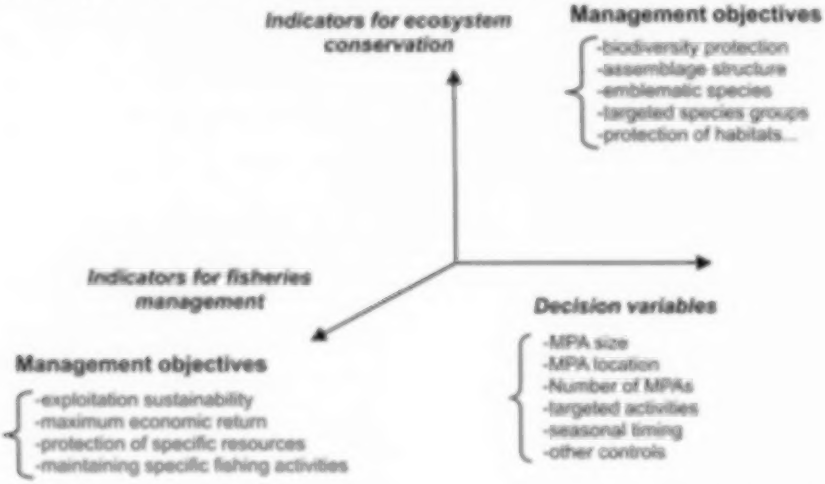
Third, alternative hypotheses about management and states of nature may be explored using dynamic models. Previous workshops with MPA managers (Pelletier 2005) evidenced the importance of testing scenarios for MPA managers; what would happen if the zoning in the MPA were modified, or in the case of changes in controls on fishing activities either within or outside the MPA? Obviously, these questions cannot be addressed through empirical approaches unless under a large-scale manipulation in the framework of adaptive management (Walters 1997). In addition, assessing and comparing the consequences of management measures other than MPAs from empirical approaches is not easy from either ecological or social perspectives (some measures may have harmful consequences) or from a scientific standpoint (replicates would be needed).

Last, empirical indicators are directly tied to monitoring. Sampling protocols may then be optimized or at least adapted to requirements on indicators' precision and accuracy (Benedetti-Cecchi 2001).

Possible contributions of empirical analyses to dynamic models

Empirical analyses provide ground truth that could be used for validating dynamic models. Hence, abundance indices collected during monitoring programs could be confronted to abundances calculated from dynamic models to help model calibration. For instance, UVC and catch data obtained from a monitoring program in a Corsican MPA have been used to calibrate an application of the ISIS-Fish model (D. Pelletier, unpublished data, www.liteau.ecologie.gouv.fr/article.php?id_article=68). This is achieved by calibrating model outputs with respect to field data by, e.g., minimizing the discrepancy between model outputs and data through the implementation

Fig. 1. Conservation and fisheries-related indicators for decision-making about marine protected areas (MPAs). Only ecosystem conservation and fisheries management issues are considered. It illustrates the multiplicity of management objectives within each general objective and the multiplicity of possible controls for management design. Several indicators are thus needed for assessing the performance of MPAs for ecosystem conservation and for fisheries management.



of numerical algorithms, such as the simplex or genetic algorithms (S. Mahévas, IFREMER, Dept. EMH, BP 21105, F-44311 Nantes, France, unpublished data).

For this purpose, it is important that model scales are consistent with the scale at which ecological and fisheries data are collected. However, models should also be considered as tools for integrating knowledge, and local information may be incorporated in a larger-scale model, thus illustrating the potential for scale transfer through modelling. This scale transfer refers not only to spatial aspects, but also to the integration of information about system components and to temporal integration.

In particular, empirical approaches provide for estimations of variance components and effect sizes, i.e., the magnitude of the MPA effect that is to be detected through monitoring (Underwood 1997). These estimates may be used on dynamic models to quantify spatial and temporal variability.

Possible contributions of dynamic models to empirical analyses

The spatial and temporal integration of population and exploitation dynamics provided by dynamic models may be interesting for empirical approaches for several reasons. First, as the dynamic models used for MPA assessment are generally fishery-oriented, they can provide estimates of fishing intensity to be incorporated in empirical analyses. Proxies for fishing intensity are more readily obtained from models than from direct measures of fishing effort, which raises the problem of effort standardization. The need to account for fishing intensity in empirical assessments of MPA effects has been underlined in several instances (Russ 2002; Micheli et al. 2005), but to our knowledge, no assessment quantitatively accounting for fishing pressure has been published yet. This may also be explained by the fact that the majority of studies deal with binary comparisons of no-take versus unprotected areas. As many MPAs established are indeed MUMPAs with a range of fishing controls following a zoning plan, the need for assessing MPA effects at multiple protection levels will likely increase in the near future.

Second, as they integrate several processes affecting fish populations, both biological and fisheries-related, mathematical models allow investigation of key processes of dynamics. This may be useful for building hypotheses about MPA effects and spatio-temporal patterns of resources at model resolution, the latter being generally chosen to capture population and exploitation features. Preliminary modelling work may thus facilitate to some extent the design of monitoring programs, in particular to account for seasonal and spatial variations in resources and fishing. Identifying which specific parameters of dynamic models are sensitive and thus require good estimation would be valuable to set up priorities for empirical studies. Which parameters are important largely depends on the model, so that it is difficult to derive general guidelines on the matter. Conducting sensitivity analysis when exploring different conservation strategies is rarely done in practice. In the case of complex simulation models, sensitivity analysis must rely on simulation experiments involving combinations of the scenarios tested, e.g., a range of MPA designs, and of possible parameter values for the uncertain parameters of interest. Appropriate simulation designs may be constructed to reduce the number of simulations. Statistical analyses adapted to the design are then used to interpret simulation outcomes and conclude to the interest of each scenario while taking into account uncertainties (Saltelli et al. 2000). These techniques were used by Drouineau et al. (2006) to compare an MPA with other fisheries management options in the case of the Bay of Biscay mixed fishery while identifying critical biological parameters.

More generally, the confrontation of empirical analyses and dynamic models is easier if the scales of data collection and model resolution are compatible. Because empirical approaches mostly pertain to local assessment, their integration with models would be facilitated by large-scale surveys and regional approaches. In addition, moving from local assessment to system-wide assessment is particularly needed in the perspective of monitoring MPA networks.

In the light of the previous considerations, framing methodological issues in the perspective of designing valid indicators of MPA effects would be beneficial, as it would guide toward improved statistical assessments and more realistic models, with the view of setting up monitoring programs. In particular, the issue of shifting baselines (Jackson et al. 2001) could be explicitly handled in collaboration with MPA managers.

Compared with other fisheries management questions, which up to now mostly rely on model-based approaches, experiences with empirical assessments of MPAs shed different light into indicator issues. They illustrate the multiple sources of variability inherent in the data that may preclude the detection of fishing or protection effects, which is of primary importance for constructing reliable indicators (Nicholson and Jennings 2004). In particular, they show the consequences for the estimation of fish abundance of several nested sources of spatial variation, in relation with (*i*) changes in habitat occurring at several scales, from local substrate to essential habitats, and (*ii*) anthropogenic pressure ranging from variation in fishing effort at the fisher level to regional regulations via MPA zoning.

MPA management

As mentioned in the Introduction, the present article was deliberately oriented toward the identification of indicators for testing hypotheses about MPA effects. This is a first step, as conservation and fisheries-related effects of MPAs are not yet fully understood and evidenced, and there is no consensus about what MPAs can achieve overall for ecosystems and fisheries.

Our study did not include economic and social effects of MPAs on fishing and other human activities. However, previous work reviewing field analyses of economic and social effects of MPAs (Pelletier et al. 2005) and bioeconomic models (Pelletier and Mahévas 2005) leads us to think that much of the above considerations remains valid for the assessment of the socio-economic effects of MPA implementation through either mathematical models or empirical evidence. At present, the relative scarcity of empirical studies concerning these effects is problematic for discussing indicators further.

Many MPAs are being established or are in project, and new monitoring programs should avoid the flaws already identified. Because indicators are derived from observations, whether directly (empirical indicators) or indirectly (model-based indicators), their information requirements should form the basis for designing monitoring programs.

Indicators for MPA-based management are not only spatial versions of indicators that may be used for other fisheries management issues. Although models rely on conventional population dynamics, exploitation features, and fishers' behaviour, the variety of possible MPA designs make it a complex, multidimensional issue compared with other management measures. Empirical approaches illustrate the diversity of ecological effects of MPAs, and consequently several indicators are needed. We proposed a list of indicators for several key MPA effects; they could be implemented, and their performance should be further evaluated.

In a second step, these indicators should be used by managers for improving the effectiveness of MPA management strategies, e.g., through adaptation of zoning or regulations, and also for reporting on MPA effectiveness (then referring to the accountability of management, Ehler 2003).

The transition toward indicators for decision support would require integrating them in the light of MPA management objectives while accounting for performance criteria linked to decision making (Fig. 1). Management objectives should thus be made explicit by MPA managers and fisheries managers, so that scientists are able to formalize them and propose appropriate indicators (Claudet and Pelletier 2004). Indicators could be scored by managers, and other stakeholders with the help of scientists. Discussions about indicators for MPA assessment have for instance been organized in the Liteau-AMP research project (Pelletier 2005) during several workshops gathering MPA managers and scientists. More generally, involvement of stakeholders is to be developed. This is for instance part of the program of work of the ongoing European research projects PROTECT (www.mpa-eu.net/) and EMPAFISH (www.um.es/empafish/) and of the PAMPA research project (www.liteau.ecologie.gouv.fr/article.php?id_article=153). In other contexts, the collaboration of local communities to MPA monitoring provides additional knowledge and contributes to a better social acceptance of MPA projects (Wells and White 1995; Elliott et al. 2001). Developing indicators for a better assessment of MPA effectiveness thus requires not only methodological contributions but also a clear appraisal of management objectives and of human resources allocated to monitoring.

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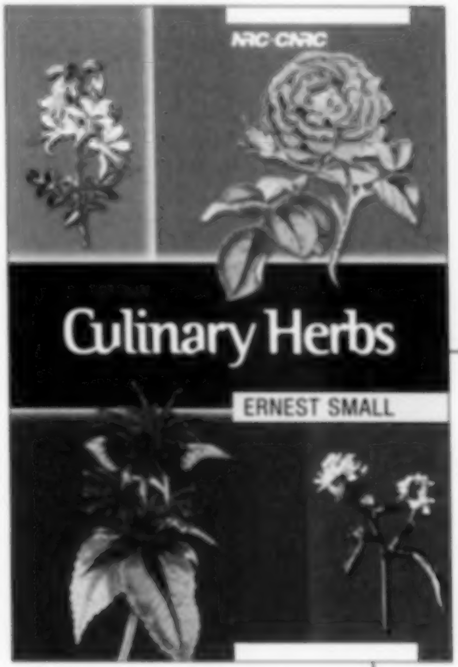

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